UNIVERSITÉ DU QUÉBEC À MONTRÉAL

LA RÉPONSE DES COMMUNAUTÉS DE CARABES À L'AMÉNAGEMENT ÉCOSYSTÉMIQUE DANS LA FORÊT BORÉALE MIXTE DE L'OUEST DU QUÉBEC

MÉMOIRE
PRÉSENTÉ
COMME EXIGENCE PARTIELLE
DE LA MAÎTRISE EN BIOLOGIE

PAR
CHRISTOPHER D O'CONNOR

JANVIER 2009

UNIVERSITÉ DU QUÉBEC À MONTRÉAL

GROUND BEETLE RESPONSE TO NATURAL DISTURBANCE-BASED MANAGEMENT AND CONVENTIONAL SILVICULTURE IN THE BOREAL MIXEDWOOD FOREST OF WESTERN QUÉBEC

THESIS
PRESENTED
AS A PARTIAL REQUIREMENT
FOR THE MASTER IN BIOLOGY

BY
CHRISTOPHER D O'CONNOR

JANUARY 2009

AVANT-PROPOS

Chapters one and two are in preparation for submission to peer-reviewed journals.

My contribution to chapter one is the collection of pitfall trapping data in 2006 and 2007, conception and design of pitfall trapping in wildfire sites, and collection and design of transects and timed collections. I identified approximately 95% of the carabid specimens (insect identifications for the 2004 collection were started by Tim Work), confirmed all specimens, and conducted all data standardizations and analysis. Pitfall collections in 2004 were conducted by Elise Bolduc from McGill University and in 2005 by Tim Work. Tim Work provided project support and guidance throughout the data collection, analyses, and writing of the articles. Regional and detailed maps were created by Mélanie Desrochers, GIS specialist for the Centre for Forest Research. Information about the location, species composition, and burn severity of the Baker Lake fire in Ontario were provided by Dr. Sybille Haeussler and Dr. Yves Bergeron. Access to the Canadian Forest Service Laurentian Forestry Centre insect collection was provided by Dr. Jan Klimaszewski. Access to the Université de Montréal insect collection was provided by Ms. Louise Cloutier.

Chapter two is based on a subset of the pitfall collection data from chapter one and environmental data provided by Dr. Suzanne Brais and the Lake Duparquet research and teaching forest. Dr. Brais also provided access to the facilities of the Lake Duparquet research station and SAFE project.

Financial support for both chapters came from Dr. Suzanne Brais, Dr. Timothy Work, The Fulbright Foundation for Educational exchange between the US and Canada, and the Lake Duparquet Research and Teaching Forest.

Acknowledgements

I would like to thank my academic advisor Dr. Timothy Work for his tireless support, editing of the preliminary versions of this document, friendship, and guidance. Dr. Suzanne Brais, director of the SAFE project, for her help with comparative datasets and background information on SAFE. Dr. Sybille Haeussler for providing coordinates for aspen wildfire sites. The members of my committee Dr. Jan Klimaszewski, Dr. Yves Bergeron, and Dr. Pierre Drapeau, the members of my lab and field assistants: Annie Hibbert, Simon Paradis, Felix Longpré, David Gervais, Marie-Ève André, Annie Cavanaugh, Simon Laberge-Gaudin, and all the others who helped along the way: Melanie Desrochers, Danielle Charron, Daniel Lesieur, and Raynald Julien.

TABLE DES MATIÈRES

LISTE DES FIGURES

LISTE DES TABLEAUX

RÉSUMÉ

L'aménagement forestier écosystémique (AFE) est perçu comme une alternative plus favorable pour l'environnement que la sylviculture traditionnelle dans les forêts d'Amérique du Nord et ailleurs. Les études précédentes en forêt boréale de l'est du Canada démontrent la capacité de l'AFE à émuler les caractères structuraux des peuplements dans plusieurs stades de succession; mais l'impact de l'AFE sur la biodiversité, particulièrement sur les organismes cryptiques comme les insectes et les autres composantes sensibles de l'écosystème n'a pas bien été étudié. Les coléoptères terrestres « carabes » ont des associations fortes quant au type de couvert de la forêt, aux conditions de microhabitats et aux structures du terrain. Ils constituent donc de bons indicateurs de changements au niveau de l'écosystème et des effets de l'AFE. Dans cette étude, nous utilisons la réponse des communautés de carabes pour tester quatre traitements sylvicoles inspirés par l'AEF sur l'abondance et diversité des coléoptères en relation aux stades de succession (peupler faux-tremble, mixte, ou conifère) et feu naturel. L'étude a été réalisée sur le site SAFE (sylviculture et aménagement forestier écosystémique) dans le sud-ouest de la forêt boréale du Québec. L'expérience vise à comparer une série de méthodes sylvicoles alternatives à la sylviculture commerciale et des forêts témoins à évaluer leur capacité à maintenir la biodiversité, la structure de la forêt et les fonctions de l'écosystème. Nous avons récolté 14 153 carabes représentant 49 espèces pendant les étés 2004 à 2007. L'analyse multivariée de la composition des communautés de carabes a démontré des différences entre les stades de succession et les différents types de traitements. Nous avons trouvé des assemblages distincts de carabes associés 1) aux coupes-totales dans chaque peuplement, 2) aux brûlés prescrits, 3) au feu naturel, et 4) entre les peuplements de grande rétention et les témoins non-coupés. La distribution spatiale des coupes partielles (dispersée ou trouée) et le niveau de rétention sont les facteurs importants qui déterminent les assemblages dans les forêts mixtes et décidues. Bien que les résultats préliminaires supportent le type d'aménagement « par cohortes » utilisé par SAFE, des suivis à long terme seront nécessaires afin de déterminer les effets de l'aménagement sur les assemblages de carabes. Les différences entre les assemblages de carabes trouvés dans les coupes-totales, les brûlés prescrits et le feu naturel suggèrent qu'il est encore nécessaire d'améliorer les méthodes sylvicoles utilisées pour imiter le feu naturel, tel que prescrit par l'AEF.

Mots clés: Sylviculture, perturbation naturelle, biodiversité, coléoptères terrestres, débris ligneux.

ABSTRACT

Natural disturbance-based management (NDBM) has been proposed as an environmentally favorable alternative to traditional silviculture in forested ecosystems across North America and elsewhere. Previous studies in the boreal forests of eastern Canada demonstrate the ability of NDBM to emulate structural features within stands across an array of successional stages; however evaluations of the impacts of alternative harvesting practices on biodiversity, particularly of more cryptic organisms such as insects, and other sensitive components of forest ecosystems are still needed. Carabid beetles are known to have strong associations to forest cover types, microhabitat conditions and structure and are potentially useful bioindicators for evaluating the effects of NDBM. Here we use the response of carabid communities to test the effects of four silvicultural prescriptions inspired by NDBM on beetle abundance and diversity in relation to successional stage (aspen, mixedwood, or conifer-dominated) and natural wildfire. The study was conducted in the SAFE (Sylviculture et aménagement forestier écosystémique) experiment in the southwestern boreal forest of Québec. The SAFE experiment compares a suite of alternative harvesting methods to commercial silviculture and uncut control stands in order to evaluate their relative effectiveness for maintaining biodiversity, forest stand structure, and ecosystem function. We collected 14,153 carabids representing 49 species over the summers of 2004-2007. Multivariate analyses of beetle community composition demonstrated differences between successional stages and among silvicultural treatments. We found distinct carabid assemblages associated with 1) clear-cuts in each cover type, 2) prescribed burns, 3) natural burns, and 4) among successional stages of higher retention and uncut controls. Partial cutting spatial distribution (dispersed or aggregated) and level of retention were important factors determining carabid assemblages in mixed and deciduous stands. Long-term monitoring is necessary to determine lasting effects of management on carabid assemblages though preliminary results support the cohort-based NDBM model for deciduous, mixedwood, and conifer-dominated forests. Carabid assemblage differences between clear-cuts, prescribed burns, and natural fire suggest that continued improvement of silvicultural methods used to emulate fire in NDBM prescriptions is needed.

Key words: Forest management, natural disturbance, biodiversity, ground beetles, coarse woody material.

INTRODUCTION

Forest management that emulates the structure and timing of natural cycles of fire and insect outbreaks has potential to reduce the negative impacts of timber harvesting on biodiversity (Harris 1984, Hunter 1993, Bergeron and Harvey 1997, Bergeron et al. 2002, Harvey et al. 2002). By maintaining within-stand structural legacies such as woody debris, as well as a mix of stand ages across the landscape, natural disturbance-based forest management (NDBM) seeks to maintain ecosystem function and promote long-term sustainability (Bengston 1994, Spence 2001).

In the absence of human intervention, landscape heterogeneity in the boreal mixedwood forests of western Québec is maintained by fire as described by Bergeron and Dubuc (1989), Bergeron et al. (1999) and Bergeron (2000). The process begins with colonization of exposed mineral soil after fire by herbaceous disturbance-adapted plants interspersed with seedlings of jack pine (*Pinus banksiana* Lamb.), balsam fir (*Abies balsamea* (L.) Mill), black spruce (*Picea mariana* (Mill.) BSP), willows (*Salix* Spp.), and pin cherry (*Prunus pensylvanica* L.). Aspen (*Populus tremuloides* Michx.) and paper birch (*Betula papyrifera* Marsh) seedlings also colonize these sites, however vegetative suckering from established rootstock is the dominant form of these species. High clay-content hydric and mesic sites generally favor aspen and birch while sandy xeric sites favor seedlings from fire-adapted jack pine and black spruce (Bergeron and Bouchard 1983). The majority of white spruce seedlings (*Picea glauca* (Moench) Voss) originate from the first masting event following fire, though seedling establishment continues during subsequent masting years (Macdonald et al. 2001).

Canopy closure typically results in the mortality of any shade intolerant aspen or pines remaining in the understory and suppression of shade-tolerant balsam fir and spruce. As aspen or pine stems begin to senesce, they are replaced by conifers recruited from the understory or by a cycle of aspen and birch, depending on the amount of available light (Bergeron 2000). Eventually, enough fir and spruce reach

the canopy that gaps caused by spruce budworm (SBW) (*Choristoneura fumiferana* Clem.) begin to control stand dynamics (Kneeshaw and Bergeron 1998). Disturbance by spruce budworm in balsam fir-dominated forests result in an old-growth forest structure composed of shade tolerant fir, cedar (*Thuja occidentalis* L.), spruce, and birch of varying ages in a mosaic of gaps and large old stems over a dense organic soil layer that limits the recruitment of early seral species (Bergeron and Harvey 1997). At any step along the successional gradient, fire can interrupt succession and return the forest structure to a pure first cohort stand in the case of a severe fire, or a mosaic of cohorts and structures in the case of low severity or patchy fire. Gap formation from spruce budworm outbreaks is most influential to stand structure only after conifer dominance of the canopy (Bouchard et al. 2005).

Within the context of forest management, silvicultural approaches can be used to alter stand structure in order to accelerate succession, maintain a specific cohort, or emulate a stand-replacing disturbance. In mature aspen stands for example, partial cutting of the overstory with protection of advanced regeneration stimulates the release of growth-suppressed understory conifers while emulating the senescence of deciduous canopy (Bergeron and Harvey 1997, Harvey et al. 2002, Bergeron et al. 2002). In young mixed stands (100-150 years post disturbance), a series of gap cuts with snag retention can be used to emulate spruce budworm damage and old conifer-dominated forest structure while maintaining an ecologically valuable deciduous component (Bergeron et al. 2002, Harvey et al. 2002). In contrast, dispersed partial cuts limit the potential for regeneration of shade-intolerant species and cyclically maintain conifer dominance. Gap and selective harvesting in older stands (200-250 years) are used to emulate insect attack and similarly maintain a mix of soft and hardwoods in the same stand (Brais et al. 2004a). Finally, clear-cuts or low-retention cuts in all forest types emulate fire and reinitiate stand succession with natural deciduous regeneration or advanced conifer regeneration using planting and site preparation (Bergeron and Harvey 1997, Bergeron et al. 1999).

In the boreal mixedwood zone of southwestern Québec, studies conducted by Bergeron et al. (1983, 1989, 1993, 1997, 1998, 1999, 2000, 2001), Harvey et al. (2002), Brais et al. (2004a, 2004b), and their students, documented several hundred years of fire and insect disturbance history and characterized stand composition, flora, soil characteristics, decomposition and coarse woody debris (CWD) of the Lac Duparquet Research and Teaching Forest. The culmination of these studies resulted in the Sylviculture et Aménagement Forestier Écosystémique (SAFE) project that incorporates the natural disturbance regimes of fire and insect outbreaks into a series of harvesting treatments that form a NDBM prescription applied to three designated management zones.

The SAFE Project, located in the Lake Duparquet research and teaching forest (LDRTF) in the Abitibi region of western Québec (48° 86'-48° 32' N, 79° 19'-79° 30' W, Brais et al. 2004b), is a fully-replicated, stand-level experiment designed to compare a suite of alternative harvesting methods, that emulate the structural characteristics of natural disturbance, to commercial silviculture and succession. The SAFE project is comprised of deciduous, mixed, and conifer dominated stand compositions representing the three major successional stages of the mixedwood boreal zone of western Québec (Brais et al. 2004b). The complete randomized block design includes uncut controls, clear-cuts, and a series of specific treatments determined by the natural dynamics of each stand composition.

Wildfire sites used in comparisons with aspen clear-cut treatments of the SAFE project were located near Timmins, ON (48° 25' N, 81° 25' W).

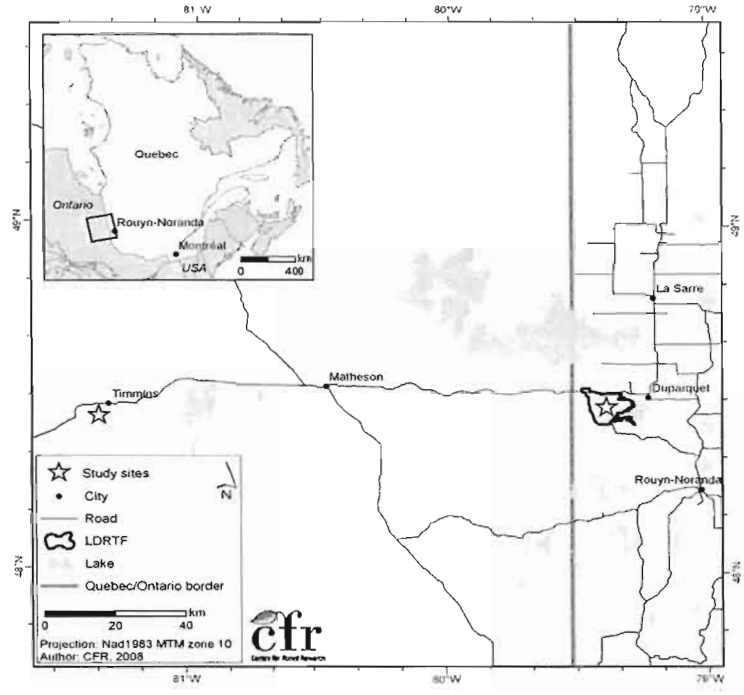


Figure I.1. Location of the Lake Duparquet research and teaching forest in Southwest Quebec and natural aspen fire sites located due west outside of Timmins, ON.

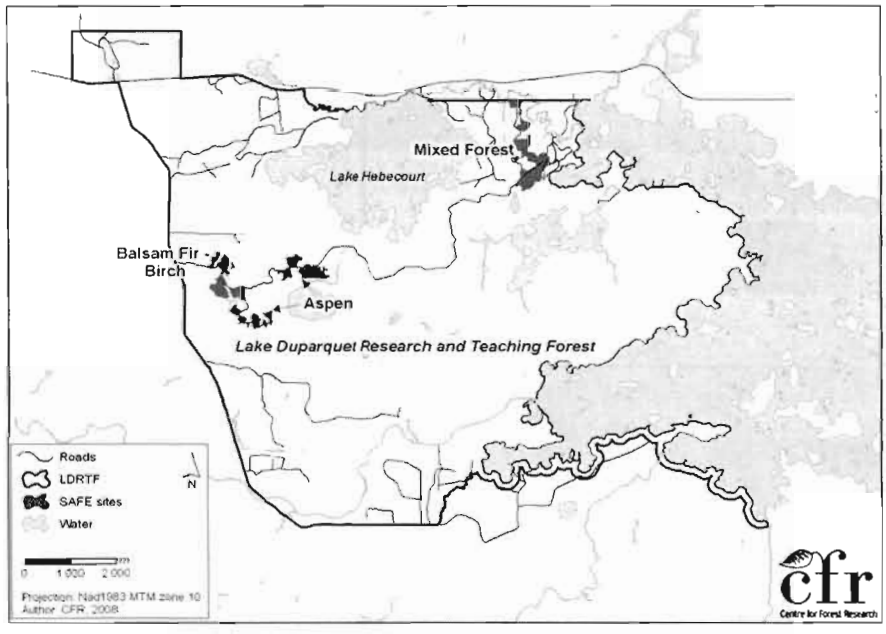


Figure I.2. Overview of the SAFE experiment in the LDRTF and placement of the three forest types used in the experiment.

This thesis is composed of two chapters assessing the impacts of the experimental management activities in the SAFE experiment on ground beetles (Coleoptera: Carabidae). We used ground beetles as indicators of forest ecosystem change because of their abundance, diversity, sensitivity to habitat change, and relative ease of sampling and identification.

In chapter one we use ground beetle assemblages to assess the impacts of the suite of natural disturbance-based management treatment options in each of the three forest types of the SAFE experiment. Experimental treatments are directly contrasted with uncut control stands, commercial harvesting treatments, and natural fire sites for their ability to maintain assemblage diversity and abundance in accordance with management goals.

In chapter two, we examine the unexpected differences between ground beetle assemblages in clear-cut treatments from early, middle, and late successional stands. Using coarse woody debris volume and decay classes, we test the role of residual structure in diversifying beetle assemblages by retaining sensitive closed canopy species in open areas.

CHAPITRE I

CARABID COMMUNITY RESPONSE TO NATURAL DISTURBANCE-BASED MANAGEMENT ACROSS A SUCESSIONAL GRADIENT OF THE BOREAL MIXEDWOOD FOREST OF WESTERN QUÉBEC

Le présent chapitre est en préparation pour être soumis à une revue. Les auteurs seront Christopher O'Connor, Timothy T. Work, et Suzanne Brais.

1.1 Introduction

In the boreal mixedwood region of western Québec, natural disturbance-based management (NDBM) has been used to successfully emulate the structure of a variety of stand types and successional stages (Bergeron and Harvey 1997, Bergeron et al. 2002, and Harvey et al. 2002). While two general arthropod studies were conducted in this region (Paquin and Coderre 1997, Paquin and Dupérré 2002), evaluations of biodiversity response to silviculture have been limited to individual stand types (see Haeussler and Bergeron 2004, Larrivée et al. 2005, and Webb et al. 2008). Response of biodiversity to NDBM in western boreal forests has been better documented (eg. Macdonald and Fenniak 2007, Work et al. 2004, Jacobs et al. 2008, Buddle et al. 2006), however flora and fauna vary considerably by region and many species are

associated with specific forest types and microsite conditions (Niemelä 1997, Uliczka and Angelstam 1999, Schmiegelow and Monkkonen 2002, Work et al. 2008).

The protection of biodiversity is emphasized as an essential component of sustainable forest management in the Montreal and Helsinki Processes which establish criteria and indicators of sustainable forestry practices (Angelstam et al. 2004). Increasingly, biodiversity has taken on the role of a quantifiable trait used to measure ecosystem health (Simberloff 1999). In managed landscapes biodiversity can be used as a comparative measure for the impacts of silvicultural methods at landscape and local scales (Lindenmayer et al. 2000). Theories on managing for biodiversity argue the virtues of fine scale (individual species) or coarse scale (environmental characteristics likely to promote species assemblages) approaches to maintaining biodiversity; while both philosophies have their merits, it is important to justify the use of one or both methods with the goals of a specific conservation plan (Poiani et al. 2000). In the boreal mixedwood zone of eastern Canada there are few identified "keystone" species with close associations to ecosystem function. This is in part due to an overall lack of information regarding the distribution and abundance of native biota, particularly understudied groups such as arthropods and fungi which comprise the majority of species diversity in forest ecosystems. Therefore it seems prudent to identify assemblages of species sensitive to forest disturbance that can be used to assess the ecosystem maintenance goals of alternative forest management.

Insects and monitoring forest change

Ground beetles (Coleoptera: Carabidae) are a diverse group associated with leaf litter, coarse woody debris, and herbaceous and canopy layer plants (Similä et al. 2002, Yu et al. 2006). Ground beetles in forested landscapes are sensitive to natural and anthropogenic disturbances such as fire and clear-cutting (Niemelä et al. 1988, 1993, 1997, 2000, 2007, Koivula 2001, 2002, Heliölä et al. 2001, Baker et al. 2004, Lemieux and Lindgren 2004, Saint-Germain et al. 2004, 2005, Work et al. 2002, 2004, Pihlaja et al. 2006, Latty et al. 2006, Buddle et al. 2006). Specific conditions

are often required for beetle oviposition and larval development (Huk and Kühne 1999); while adults may disperse widely searching for food and mates, the less mobile larval stages are more likely to be sensitive to stand-level changes (Luff 2005). Rainio and Niemelä (2003) recommend carabids for studies of ecosystem change because of their abundance, ease of capture, diversity, specific habitat affinities, and sensitivity to local and stand-level disturbance. Most carabids are considered generalist predators, and likely feed upon a variety of lower trophic groups (Hengeveld 1979). The scale invariance phenomenon noted by Briand and Cohen (1984) states that species diversity at higher trophic levels is directly proportional to that at lower trophic levels. Their findings suggest that increased diversity of predators such as carabids may indicate enhanced diversity at lower trophic levels (detritivore, fungivore, and primary producer) that directly influence ecosystem productivity and nutrient cycling. In addition, it is important to note that temperature, physical structure, and moisture gradients also affect carabid distributions (Lövei and Sutherland 1996).

Niemelä et al. (1988, 1993) and Koivula (2001) characterized carabid ground beetles in boreal ecosystems as forest, open habitat, and generalist species groups. Recently Jacobs et al. (2008) used ten species abundant in the forests of western Canada to adapt these classifications to the stages of boreal forest succession, making them directly applicable to the NDBM model. Their classification assigns species to one of five categories based on response to succession and disturbance. Forest generalists are omnipresent across stand compositions but their abundance is reduced with increasing level of canopy removal. Open habit generalists are also found across successional gradients in forest gaps and open areas and are generally promoted by removal of forest canopy. Mature deciduous forest species have peak abundance under deciduous canopy but are present in later stand compositions and are tolerant of reductions in tree basal area to a level of 50% canopy removal. Mature conifer forest species have peak abundance under a conifer canopy but are also present in earlier stages of succession and are also tolerant of minor reductions in stand basal area.

Finally old forest species occur only in old growth stands and are highly sensitive to changes in stand composition and canopy cover. A diverse landscape comprised of multiple successional cohorts and a variety of disturbance and mature forest types is thought to maintain these uniquely adapted insect assemblages (Jacobs et al. 2008).

1.1.1 Hypotheses

Here we use the composition and abundance of ground beetles to assess a suite of natural disturbance-based management silvicultural strategies in comparison to control stands and commercial harvesting treatments. We use community and species-level analyses to establish baseline assemblages associated with each stage of forest succession and to make comparisons with assemblages found in commercial harvesting, alternative silvicultural treatments, and natural fire.

The three stages of boreal mixedwood succession are characterized by distinctly different structure, dominant species, and ages, thus each successional stage is expected to host a distinct carabid assemblage (H1). Abundance and species composition of carabid assemblages is expected to respond to variation in microsite conditions influenced by forest disturbance, age, and composition changes in canopy and understory vegetation. The habitat preferences noted by Holliday (1991) further suggest that the neutral pH, fast-decomposing organic layer in deciduous stands and acidic, slow-decomposing litter layers in conifer-dominated stands will likely host different carabid assemblages.

Species assemblages in clear-cuts are generally different from those following wildfire, thus early seral beetle communities in clear-cuts are expected to be similar across all forest types and different from those in naturally burned stands (H2). In the NDBM model (Bergeron and Harvey 1997), clear-cutting replaces fire as a stand regenerating event that moves stand structure from early, mid, or late successional structure back to initial cohort deciduous regeneration. Uncut forests and open clear-cuts will likely have the greatest differences in beetle assemblages. Partial cuts

should reflect intermediate changes in insect communities along a gradient of cut severity.

Carabids typified as old forest specialists are expected to have highest concentrations in undisturbed older stands, intermediate concentrations in partial cuts, and lowest numbers in clear-cut areas where stem removal and additional site preparation used to improve stand regeneration should virtually eliminate their required habitat (H3). Based on the findings of Koivula (2001), dispersed cut stands sharing significant edge surface with closed canopy forest should show little difference in species composition but potential differences in species abundance from the neighboring closed canopy.

These hypotheses are based on applying a modified coarse filter approach (Hunter et al. 1988) to maintaining biodiversity that manages for diverse stand structures and ages instead of targeting individual species for preservation. At a finer scale, the coarse filter approach influences stand conditions by affecting within-stand elements such as woody debris, snags, canopy gaps, and accumulated organic matter important to resident flora and fauna.

1.2 Study area and design

1.2.1 Study Sites

The SAFE Project, located in the Lac Duparquet research and teaching forest in the Abitibi region of western Québec (48° 86'-48° 32' N, 79° 19'-79° 30' W, Brais et al. 2004b), is a fully-replicated, stand-level experiment designed to compare a suite of alternative harvesting methods, that emulate the structural characteristics of natural disturbance, to commercial silviculture and succession. The SAFE project includes aspen stands, deciduous-dominated young mixed stands (referred to as "mixed" throughout this paper), and older mixed stands comprised of balsam fir, paper birch, and white spruce previously subjected to multiple budworm outbreaks (referred to as "balsam fir-birch" throughout this paper) representing the major successional stages

of the mixedwood boreal zone of western Québec (Brais et al. 2004b). Each successional stage includes replicated clear-cuts, uncut controls, and specific treatments based on histories of logging, fire, and insect outbreaks unique to each stand type (Brais et al. 2004b). Aspen stands are comprised of an even-aged 84-year-old first cohort with a conifer sapling understory. Mixed forest stands are characterized by a senescing 100 year-old aspen canopy that also contains mature spruce and a well-developed balsam fir understory. Balsam fir-birch stands exhibit uneven age structure and a mix of species that have been driven by budworm-related gaps and stand succession in the 245 years since stand replacing fire.

Treatments within the aspen stands were designed to manage the aspen canopy and conifer advanced regeneration which date from the last stand replacing fire in 1923 (Dansereau and Bergeron 1993). Over the winter of 1998-99, two intensities of partial cuts and a series of three clear-cuts with different treatments of residuals were completed for comparisons with uncut controls. The 1/3 partial-cut treatment selectively thinned non-vigorous, small diameter stems to accelerate competitive thinning and encourage large stem growth. The 2/3 partial-cut treatment targeted large diameter marketable stems to maximize usable timber from the harvest and emulate large stem senescence to facilitate recruitment of conifers from the understory. The three clear-cut treatments emulating wildfire included commercial stem-only harvest (residual tops and branches left on the landscape), low-intensity controlled burn after stem-only harvest, and whole tree removal (Brais et al. 2004b).

In the winter of 2000-01, treatments were carried out on mixed stands with a canopy dominated by over-mature aspen showing signs of senescence and an understory composed of balsam fir and white and black spruce. The aspen canopy dates from the last major fire in 1910, though some of the oldest living conifer stems were dated to 175 years. Clear-cut and uncut control treatments were contrasted with two different partial-cut strategies, each removing 42-47% of forest basal area. The first partial-cut was designed to emulate aspen senescence and stimulate conifer

growth. The cut is dispersed through the experimental stand with two 5m-wide clear-cut hauling trails separated by a 5m uncut strip and 25% of stems harvested in the strips bordering (see figure from Brais et al. 2004b). The second partial-cut uses gap-cuts to emulate natural gap formation resulting from spruce budworm or other insect damage. For this treatment, the two hauling trails were widened at two points to form 16m x 20m (320 m^2) clear-cut gaps connected by the 5m wide hauling trails. The dispersed and gap cuts are designed to manage natural regeneration to favor recruitment of shade tolerant or shade intolerant saplings respectively.

Mature balsam fir-birch stands are characterized by a paper birch and white spruce canopy with a regenerating balsam fir understory interspersed with white cedar. Historical outbreaks of spruce budworm, the most recent between 1970 and 1984 (Bergeron et al. 1995), killed off the majority of mature balsam fir and diversified stand structure, age, and species composition since the last stand-replacing fire in 1760 (Brais et al. 2004b). The understory of this forest type is characterized by a build up of deadwood and demonstrates typical gap dynamics structure with standing snags and a mixture of shade-tolerant fir and birch saplings. Treatments carried out over the winter of 1999-2000 were used to compare clear-cuts with understory protection to control stands to observe conifer stand natural regeneration potential. Detailed information on site characteristics such as soil nutrients, humus layer depth, woody debris volume and accumulated leaf litter are also useful for making site and treatment comparisons however these data are not treated in this study.

Each forest type at SAFE contains three replicated blocks of each treatment and control. Experimental parcels (including controls) within each block range from 1-3 hectares and contain five 400m^2 circular permanent sampling plots with centers flagged and digitized in a GIS database.

SAFE-Wildfire comparison

A second study compared aspen clear-cut treatments of the SAFE project to a similarly aged aspen wild-fire using the sites of Haeussler (2004) in the Baker Lake area near Timmins, ON (48° 25' N, 81° 25' W). On 29 May 1997, a thunderstorm ignited a series of conifer canopy fires that covered 204 hectares and burned into adjacent mature aspen stands. Sampling plots were established in three unsalvaged aspen burn sites containing dense aspen regeneration and abundant standing fire-killed snags and fallen large woody material.

Table 1.1 provides a summary of experimental treatments in each forest type and the natural disturbance it is intended to emulate.

Table 1.1 Experimental treatments used to emulate natural disturbance

Forest type	Experimental treatment	Simulated disturbance or successional stage	Expected result
Mature aspen with sparse conifer understory	1/3 partial cut small stems	non-vigorous stems senesce from competition	Reduced competition maximizing stem diameter growth and quality
	2/3 partial cut large stems	large old stem senescence	Canopy opening to stimulate conifer growth and mixed forest structure
	Clear-cut with retained slash	fire	New aspen suckering
	Clear-cut followed by prescribed fire	fire	New aspen suckering
	Whole tree harvest (slash removed)	fire	New aspen suckering
	Natural fire	N/A	New aspen suckering
Senescing aspen, mature fir and spruce understory	40% partial cut dispersed	old stem senescence	Release of sub-canopy conifers and selection for shade-tolerant regeneration
	40% partial cut aggregated (gap)	SBW outbreak	Mixed sapling recruitment- shift to older hard and soft-wood forest structure
	Clear-cut with understory protection	fire	Aspen suckering, established conifer sapling growth release
Regenerating fir dominated by birch, spruce, and cedar	Clear-cut with understory protection	fire	Aspen and birch suckering, established fir and birch seedling growth release

1.2.2 Sampling methods

Insect sampling conducted six and seven years post silvicultural treatments accounted for adult beetle longevity of two or more years for some boreal species (Lövei and Sutherland 1996). Previous studies relying on carabid catches immediately following silvicultural treatments have encountered problems with samples containing a large number of displaced adult individuals retained from preharvest forest types (Van Dijk 1996, Koivula 2002).

Pitfall Trapping

Pitfall trapping was used to characterize species assemblages among forest types and experimental treatments. Collections in each treatment were conducted continuously over two consecutive summers to account for the seasonality of forest carabids (Reeves et al. 1983, Spence and Niemelä 1994, Werner and Raffa 2003). An accurate assessment of carabid diversity requires many traps because target organisms must randomly encounter the small sampling apparatus to be recorded (Spence and Niemelä 1994, Work et al. 2002, Oliver and Beattie 1996). Each of the five permanent sampling plots within a treatment contained two pitfall traps yielding 10 pooled samples within each of the three replicated experimental units. Details of the sampling design are summarized in Appendix A. Pitfall traps consisted of two nested 200ml disposable plastic cups with the outside cup acting as a sleeve and placeholder for the removable inside cup. Traps were filled with 20ml of Prestone® low-toxicity propylene glycol preservative solution. A 10cm x 10cm square of corrugated plastic was suspended with wire 3 cm above the trap to keep out rainwater and debris. In the field, traps were collected using a strainer lined with cotton filter-cloth. Samples were strained of preservative through the cloth and preservative was returned to the empty trap. Strained contents were then bundled in the cotton cloth with a label identifying location and time of collection, and closed with a twist tie.

Samples were held in a sealed one-gallon bucket for transport before sorting and separation into micro-centrifuge tubes filled with 70% ethanol for storage.

Sampling Effort

Sampling of arthropods in aspen stands began in 2004 with continuous sampling between 8 May and 26 August. The 2004 collection included aspen controls, partial cuts, commercial clear-cuts and experimental burns. Sampling was expanded the following year to include the aspen whole-tree removal treatment and all treatments in the mixed and balsam fir-birch stands where collections took place between 28 May and 8 September 2005. Mixed and balsam fir-birch stand sampling continued from 6 May to 23 September 2006. Aspen wildfire sites were sampled between 6 August and 23 September 2006 and from 4 May to 11 September 2007. Each of the three replicated treatment blocks within a stand contained 10 traps, yielding a total of 30 traps per treatment. A total of 390 traps were used over the thirteen treatments equating to 79,833 total trap days over the entire experiment (see Appendix A).

Specimen preparation and identifications

Samples were sorted to separate vials as carabids, other coleoptera, and spiders. Within each sample, the number of slugs, salamanders, frogs, and mammals was also tabulated. We identified carabid specimens to species using Lindroth (1961-1969) and Bousquet and Goulet (2008). Voucher specimens were verified by comparisons with the carabid collections at The CFS Laurentian Research Station and the collection of André LaRochelle at the Université de Montréal.

Individual trap catch numbers were converted to daily trap catch rates per species. This conversion standardized catches by the number of days each trap was open and corrected for disturbed or missing traps. Traps that were flooded, filled with debris, or had the lid sealed at some time during the collection period were

subjected to a trap disturbance correction formula in which the number of days the trap was running during the specified sampling period was reduced by one half to compensate for reduced trapping efficiency.

The experimental design in which silvicultural treatments were staggered over the winters of 1998, 1999, and 2000, as well as sampling in the natural aspen fire in 1997 inherently incorporated inter-annual variations in temperature and precipitation. Abildsnes and Tømmeros (2000) found pitfall trapping catches to vary from year to year and attributed this variation to differences in mean temperature. We did not attempt to account for the effects of year to year climate differences in pitfall trapping catch comparisons though it is important to note that temperature variation is likely one source of error in comparisons between carabid species assemblages collected from different years.

1.2.3 Analytical methods

Estimated Species Richness and Rarefaction

Pooled daily catch rates were used for direct comparisons of beetle abundance by forest type and treatment and were tested for significant differences with Kruskal-Wallis nonparametric analysis of variance.

We used rarefied species richness (Simberloff 1978, Colwell and Coddington 1994, Gotelli 2001) to directly compare carabid assemblages and species turnover among stand compositions and silvicultural treatments. Rarefaction of pooled sample abundance uses random subsamples of increasing size to generate an estimate of increasing species richness with sampling effort (Gotelli and Colwell 2001). Curves were generated using the "rarefy" function in the R package VEGAN version 1.6-10 (Oksanen et al. 2005). Individual-based rarefaction code was adapted from Jacobs (2006) to calculate a rarefaction estimate for every 50 individuals within each treatment. Comparisons between species accumulation curves were based on 600 individuals, which was the minimum number of beetles collected in two-years of

sampling in any treatment. Complete rarefaction curves for each treatment (from zero to the total beetle count) were reported to assess whether samples adequately captured species richness (attained an asymptote) within a given treatment.

Community response to silvicultural treatments

For community analysis, species catches from individual traps were pooled by treatment replicate and then standardized by the number of trap days, yielding a daily catch rate for each species within a treatment replicate (example: 1.03 *P. pensylvanicus* were collected each day of trapping within aspen control replicate one). The catch rates from each of the three replicates of a given treatment were used in multivariate analysis of community differences among forest types and treatments. Community analyses were designed to test each hypothesis (assemblage differences by forest type and treatment) and to compare carabid assemblages found in the suite of managed treatments to natural assemblages in control and wildfire stands. Because our data did not meet the assumptions of traditional ANOVA or MANOVA designs, we used a non-parametric multivariate ANOVA homologue that permits the use of ecological distance measures (McArdle and Anderson 2001, Anderson 2001). Permutation based ANOVA (PERMANOVA) addresses analytical problems commonly encountered in ecology including zero-inflated data (Legendre and Legendre 1998, McCune and Grace 2002), non-normality (McCune and Grace 2002) and low number of replicates. This method generates a pseudo F-statistic from the response variables (carabid species catch rates by treatment) and tests it against a row-permuted randomized F to generate a p-value by Monte-Carlo simulation. Computed distances between response variables within the same treatment and among treatments are displayed as a table following each test. We used global and pair-wise PERMANOVA tests to address our hypotheses by comparing carabid catch rates and similarity of species composition measured as Bray-Curtis distance in: 1) the three control forest types; 2) the five clear-cut treatments and aspen wildfire; and 3) the suite of treatments within each forest type. Wildfire sites were also included in

the model testing for significant differences between aspen treatments. Species found in fewer than 5% of the sampling units (any species found in only 1 of the 39 pooled samples, following the recommendations of McCune and Grace 2002 and Work et al. 2004) were excluded from the community analysis. The numbers of species included in each PERMANOVA test were: control forest, 17; clear-cut and fire, 34; aspen stands, 31; mixed stands, 23 and spruce stands, 16. Raw data were quad-root transformed to reduce the several orders of magnitude difference between rare and abundant species before conversion to a site by site Bray-Curtis distance matrix. Bray-Curtis was selected as an appropriate measure for community analysis based on the large number of zeros in the dataset and the desire to compare communities using species composition and diversity (Legendre and Legendre 1998, Legendre and Gallagher 2001, McCune and Grace 2002). Full model and pair-wise comparison PERMANOVA tests were run using 9999 permutations and a random integer seed for each analysis in the FORTRAN package PERMANOVA 6 (Anderson 2005). Statistical tests were deemed significant at a confidence level of $p \leq 0.05$ for single comparisons and were corrected using the Bonferroni method ($p \leq 0.05/n$ comparisons) for multiple comparisons.

Regression tree community model

While PERMANOVA provided a means to evaluate the statistical significance of our hypotheses, further detailed characterizations of the differences in species assemblages among treatments were warranted. We used a multivariate regression tree (MRT) (Breiman et al. 1984, De'ath 2002a) to summarize the findings of individual PERMANOVAs and relate beetle communities to forest types and treatments. MRT is a constrained community analysis method that is not subject to the underlying linear or unimodal distribution assumptions of eigenvalue methods, such as redundancy analysis (RDA) or canonical correspondence analysis (CCA), and can account for interactions between environmental variables. As the number of data splits increases, more variance in the response table is explained. Selection of the

model that minimized cross-validation error was used to prevent over-fitting (incorporation of too many splits in the MRT model). Data transformations and computation of the distance matrix followed the same procedures used in PERMANOVA. The R program for statistical computing version 2.7.1 (R core development team 2008) was used for the analysis. Bray-Curtis distance measures were calculated using the VEGAN package 1.6-10 (Oksanen et al. 2005) and regression trees were constructed using the MVPART package version 1.2-4 (De'ath 2002b). The MRT used 1000 permutations for tree selection and a matrix of 37 species using the variables treatment and cover type.

Species affinities for cover types and treatments

An indicator species analysis was conducted using the Dufrêne and Legendre (1997) method where terminal nodes of the MRT (treatment-cover-type interactions) were used as grouping variables. In this study we considered species with indicator values between 30 and 100 and a p-value < 0.05 to be useful indicators. The analysis used the MRT species matrix and was carried out in the "duleg" function of the LABDSV package (Roberts 2004) for "R" with a Monte Carlo test of significance of observed maximum indicator value for each species using 5000 permutations.

1.3 Results:

1.3.1 SAFE collection summary

We collected 14,056 individual carabids representing 47 species and approximately 54,400 other coleoptera, 24,900 spiders, 27,200 slugs, 125 small mammals, 98 frogs, and 23 salamanders. Carabid collections were dominated by five species: *Pterostichus pensylvanicus* (LeConte) (29.2%), *Synuchus impunctatus* (Say) (16.8%), *Agonum retractum* (LeConte) (14.2%), *Pterostichus coracinus* (Newman) (8.4%) and *Spheroderus nitidicollis* (Guérin-Méneville) (7.8%); each of which was represented by more than 1000 individuals. Four more species were represented by more than 500 individuals and together these 9 species account for 94% of the total

carabid abundance of the study. The remaining 6% of carabid abundance was comprised of 29 species with intermediate abundance of 2-162 individuals, and nine species with a single individual collected (Figure 1.1). Complete pitfall trapping results by species and treatment are summarized in Appendix C.

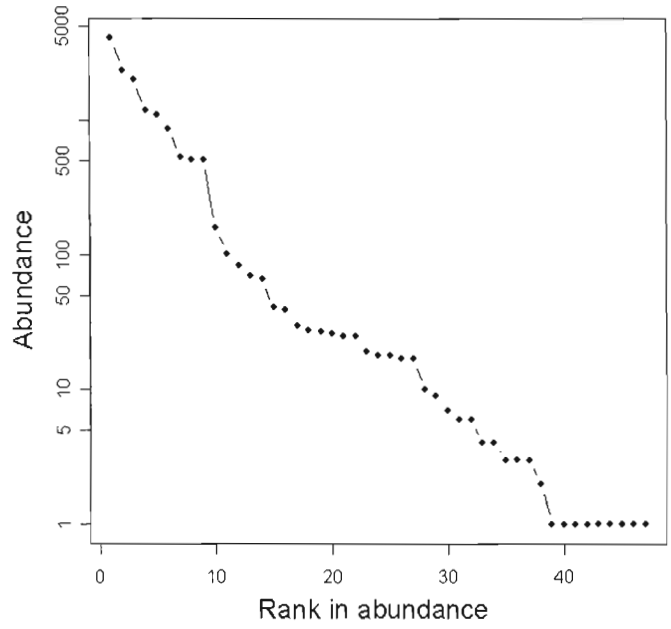


Figure 1.1 SAFE species rank in abundance of the 47 species from pitfall trapping shows a log-linear decline for the first 38 species and a tail of nine species with only one individual.

1.3.2 Species richness and abundance among successional stages

In aspen stands, carabid catch rates (abundance) decreased with harvesting intensity (Kruskal-Wallis $\chi^2 = 7.682$, p= 0.005 for controls, partial-cuts, and wildfire versus clear-cuts, prescribed burns and whole tree removal). Uncut controls, wildfire, and partial cuts had comparable high catch rates ($\chi^2 = 3.000$, p=0.392, see figure 1.2). In mixed stands the trend was similar for average catch rates, however Kruskal-Wallis test results were not significant for controls and dispersed cuts versus gap and clear-cuts ($\chi^2 = 1.447$, p=0.229). As in aspen stands, balsam fir-birch carabid catch rates were significantly lower in clear-cut treatments than in controls ($\chi^2 = 3.857$, p=0.0495). Overall control stands had similar catch rates regardless of stand

composition. Clear-cuts generally had lower catch rates than partial cuts or controls with the exception of mixed stands, where gap-cuts had the lowest carabid catch rates.

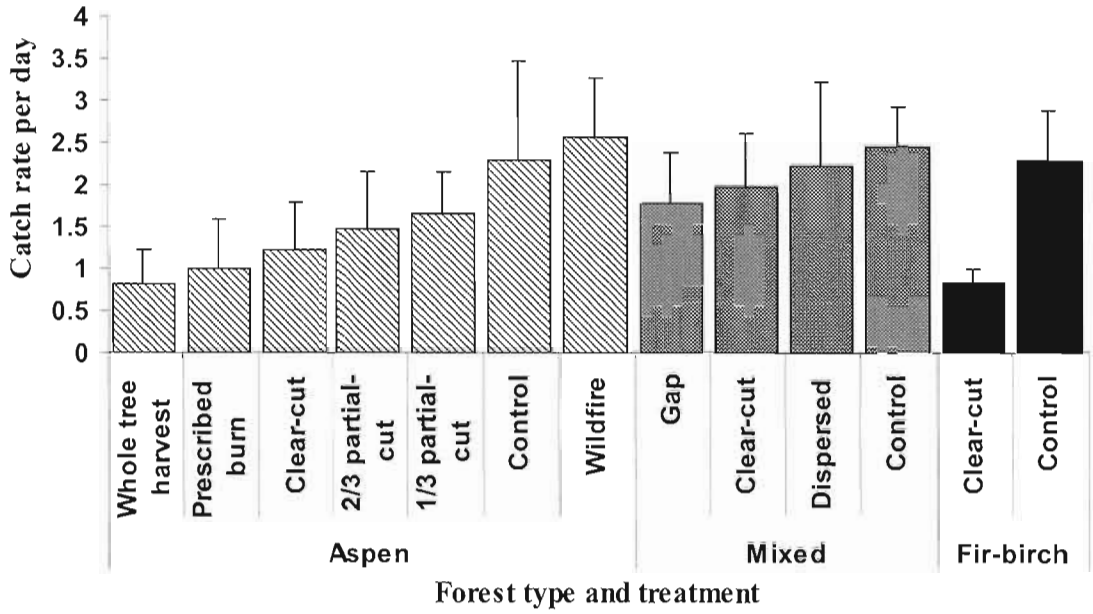


Figure 1.2 Average daily catch rate pooled by forest type and treatment. Error bars are one standard deviation.

Rarefaction of pooled sample abundances

Differences in estimated species richness were greatest among treatments in aspen and balsam fir-birch stands (Fig. 1.3a, b, c). Estimated species richness was highest in clear-cuts (aspen, 24 species; mixed, 19 species; balsam fir-birch, 21 species) and prescribed burns (29 species), and lowest in control stands (aspen, 15 species; mixed, 14 species; balsam fir-birch, 13 species). Estimated richness in wildfire sites (21 species) was intermediary between aspen clear-cuts (24 species) and partial cuts (17 species). In contrast to the carabid catch rates mentioned above, estimated species richness increased with level of disturbance in all cover types.

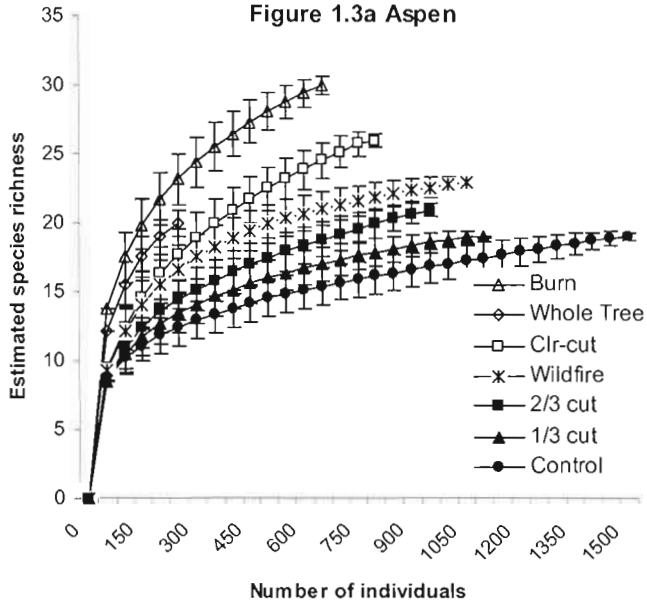


Figure 1.3a Aspen
Estimated species richness
Number of individuals
Burn
Whole Tree
Clr-cut
Wildfire
2/3 cut
1/3 cut
Control

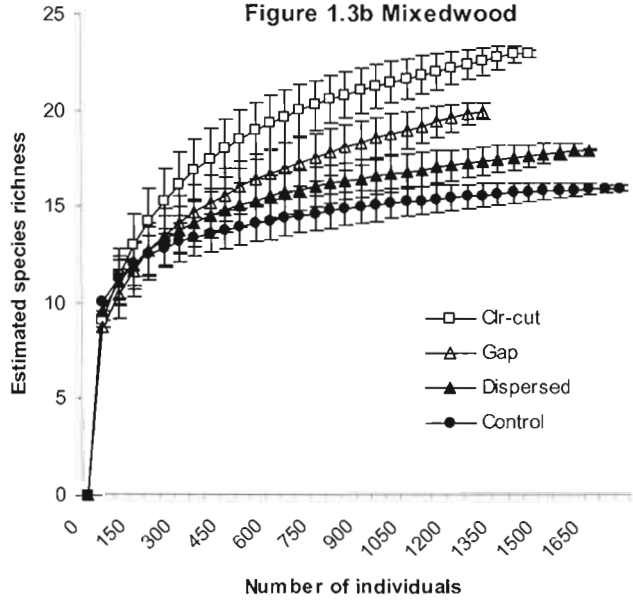


Figure 1.3b Mixedwood
Estimated species richness
Number of individuals
Clr-cut
Gap
Dispersed
Control

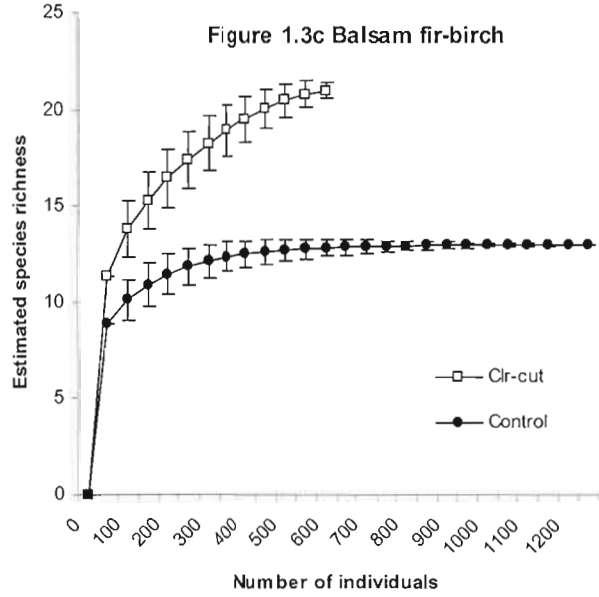


Figure 1.3 a, b, and c. Rarefaction of pooled sample abundance by aspen, mixed, and balsam fir-birch forest type. Subsamples used an interval of 50 individuals. Error bars are ±1SD of the permuted value of each subsample. Clear-cut treatments and gap cuts (unfilled shapes), wildfire (X), and dispersed-cuts and controls (solid shapes) are listed in order of rarefied species richness.

After the first 750 individuals, estimated richness in control stands increased by one new species with the addition of approximately 250 individuals in aspen stands, 500 individuals in mixed stands, and 600 individuals in balsam fir-birch stands, suggesting that sampling was sufficient to characterize carabid assemblages in uncut controls. In contrast, the total collections from aspen prescribed burn, whole tree removal, and balsam fir-birch clear-cut treatments were fewer than 750 individuals. Estimated richness curves did not reach a clear asymptote in these treatments. Differences between rarefaction curves generated from control and clear-cut stands suggest a strong treatment effect on species richness and overall abundance.

1.3.3 Community differences among forest types and treatments

Using global tests to distinguish beetle assemblages among treatments and cover types we found significant differences in carabid composition between cover-types in uncut-stands and between cover types and treatments in clear-cuts and wildfire. Within stands of similar composition, treatments had a significant effect on beetle assemblages in aspen and balsam fir-birch stands; however treatment effects in mixed stands were not significant after correction for multiple comparisons (Table 1.2).

Table 1.2 Single factor PERMANOVA tests of hypotheses (H) for carabid assemblage differences by stand composition and treatment

Test	Source	df	SS	MS	F	P(perm)	P(MC)
Controls (H 1)	Forest type	2	994.3755	497.1877	4.4087	0.0039	0.0070**
	Residual	6	676.6423	112.7737			
	Total	8	1671.0178				
Clear-cuts and wildfire (H 2)	CC treatment	5	7152.7841	1430.5568	3.0973	0.0001	0.0002**
	Residual	12	5542.5130	461.8761			
	Total	17	12695.2971				
Aspen stands (H 3)	Treatments	6	6202.0912	1033.6819	2.4610	0.0004	0.0012**
	Residual	14	5880.4609	420.0329			
	Total	20	12082.5521				
Mixed stands (H 3)	Treatments	3	1456.9338	485.6446	2.6309	0.0081	0.0220*
	Residual	8	1476.7389	184.5924			
	Total	11	2933.6727				
Balsam fir-birch stands (H3)	Treatments	1	753.8945	753.8945	6.3056	0.0993	0.0156**
	Residual	4	478.2403	119.5601			
	Total	5	1232.1347				

* Denotes significant difference uncorrected for multiple comparisons
** Denotes significant difference corrected for multiple comparisons

With the exception of balsam fir-birch stands, p-value correction for the multiple comparisons used in pair-wise tests rendered differences between compared carabid assemblages not significant at a level of $p < 0.05$. Uncorrected p-values indicating significant differences between carabid assemblages are included in pair-wise comparisons but should be interpreted with caution.

Pair-wise tests in uncut stands indicated that carabid assemblages in mixed forests differed from those found in the two other forest types. No difference was found between beetle assemblages in aspen and balsam fir-birch stands (Table 1.3). Variation among stand replicates (measured as Bray-Curtis distance) was greatest in aspen, intermediate in balsam fir-birch, and least in mixed forests (numbers in bold, Table 1.4).

Table 1.3 PERMANOVA Pair-wise tests among control stands

Group	df	t	P(perm)	P(MC)
Aspen x Balsam fir	5	1.7681	0.0983	0.0795
Aspen x Mixed*	5	2.4006	0.1057	0.0228*
Balsam fir x Mixed*	5	2.1390	0.0962	0.0295*

* indicates significant difference between groups uncorrected for multiple comparisons

Table 1.4 Average Bray-Curtis distance within/between control stands

Forest Type	Aspen	Balsam fir	Mixed
Aspen	**18.846**		
Balsam fir	20.849	**13.096**	
Mixed	24.624	18.047	**10.741**

In pair-wise tests of clear-cuts and wildfire, we found carabid composition differed in aspen, mixed, and balsam fir-birch clear-cuts (Table 1.5). Carabid composition in wildfire was different from aspen clear-cuts, prescribed burns, and balsam fir-birch clear-cuts, but not mixed clear-cuts or whole tree removal. While carabid assemblages in prescribed burns were not distinguishable from those in aspen clear-cuts or whole-tree harvesting, the variation between treatment replicates was also highest in these three treatments (Table 1.6). In clear-cut and wildfire plots, variation among treatment replicates was highest in aspen stands, intermediate in mixed stands, and lowest in balsam fir-birch stands.

Table 1.5 PERMANOVA pair-wise comparisons of clear-cuts and natural fire

Groups	df	t	P(perm)	P(MC)
Burn x Whole tree	5	1.0608	0.6019	0.3773
Burn x Aspen Cc	5	1.4222	0.0998	0.1413
Burn x Fir Cc*	5	2.5503	0.1030	0.0157*
Burn x Mixed Cc*	5	2.4187	0.0993	0.0209*
Burn x Wildfire*	5	2.4692	0.1040	0.0148*
Whole tree x Aspen Cc	5	0.6321	1.0000	0.8178
Whole tree x Fir Cc	5	1.3822	0.2005	0.1873
Whole tree x Mixed Cc	5	1.5294	0.1025	0.1099
Whole tree x Wildfire	5	1.5342	0.1022	0.1091
Aspen cc x Fir Cc*	5	1.8871	0.1052	0.0415*
Aspen cc x Mixed Cc*	5	1.8807	0.0989	0.0492*
Aspen cc x Wildfire*	5	1.8742	0.0993	0.0432*
Fir cc x Mixed Cc*	5	2.5115	0.1047	0.0154*
Fir cc x Wildfire*	5	2.6326	0.1062	0.0148*
Mixed cc x Wildfire	5	1.7324	0.0937	0.0779

* indicates significant difference between groups uncorrected for multiple comparisons

Table 1.6 Average Bray-Curtis distance within/between harvest and fire treatments

Treatment	Burn	Whole tree	Aspen cc	Spruce cc	Mixed cc	Wildfire
Burn	**30.023**					
Whole tree	37.755	**43.870**				
Aspen cc	36.087	34.530	**32.767**			
Spruce cc	42.831	37.727	36.929	**19.803**		
Mixed cc	43.613	42.260	38.656	36.418	**23.827**	
Wildfire	45.630	43.143	39.668	39.182	31.341	**24.602**

Pair-wise tests of treatments in aspen stands indicated carabid assemblage differences between prescribed burns and partial cuts, controls, and wildfire (Table 1.7). Carabid assemblages did not differ significantly between clear-cuts, partial-cuts, and controls. Community similarity was higher among 1/3 and 2/3 partial cuts and controls than any other treatments within aspen stands. Beetle composition in wildfire differed from all silvicultural treatments except whole tree removal (extreme variability among replicates) and uncut controls. Average variation among replicates in aspen treatments was highest in whole tree harvest, prescribed burning, and clear-cuts, intermediate in wildfire and uncut controls, and lowest in partial-cutting treatments (Table 1.8).

Table 1.7 PERMANOVA pair-wise tests among aspen treatments

Groups	df	t	P(perm)	P(MC)
1/3 part x 2/3 part	5	0.7936	0.7035	0.6054
1/3 part x Burn*	5	2.4501	0.1057	0.0149*
1/3 part x Whole tree	5	1.1953	0.3047	0.2645
1/3 part x Com Cc	5	1.5447	0.1015	0.1064
1/3 part x Control	5	0.6505	0.8006	0.7130
1/3 part x Wildfire*	5	2.3224	0.0973	0.0269*
2/3 part x Burn*	5	2.3302	0.1000	0.0237*
2/3 part x Whole tree	5	1.1299	0.3033	0.3185
2/3 part x Com Cc	5	1.3092	0.1003	0.1875
2/3 part x Control	5	0.8886	0.4971	0.5234
2/3 part x Wildfire*	5	2.0911	0.1014	0.0342*
Burn x Whole tree	5	1.0612	0.5940	0.3701
Burn x Com Cc	5	1.4406	0.1984	0.1342
Burn x Control*	5	2.3583	0.0989	0.0203*
Burn x Wildfire*	5	2.4978	0.1066	0.0147*
Whole tree x Com Cc	5	0.5919	1.0000	0.8452
Whole tree x Control	5	1.1060	0.2058	0.3356
Whole tree x Wildfire	5	1.5334	0.0980	0.1153
Com Cc x Control	5	1.4229	0.1986	0.1443
Com Cc x Wildfire*	5	1.9427	0.1013	0.0388*
Control x Wildfire	5	1.6865	0.0978	0.0776

* indicates significant difference between groups uncorrected for multiple comparisons

Table 1.8 Average Bray-Curtis distance within/between aspen treatments

Treatment	1/3 part	2/3 part	Burn	Whole tree	Com Cc	Control	Wildfire
1/3 part	**19.566**						
2/3 part	18.568	**20.805**					
Burn	41.618	40.553	**30.162**				
Whole tree	36.259	35.643	37.825	**43.870**			
Com Cc	31.048	29.276	35.293	33.430	**30.849**		
Control	19.726	22.128	44.068	36.949	32.432	**24.648**	
Wildfire	34.558	32.728	45.252	42.544	38.322	31.376	**23.504**

In mixed forest, pair-wise tests of treatments showed carabid assemblages in control stands to be different from those in clear-cuts and gap-cuts (Table 1.9). Assemblage differences were not significant between clear-cuts, dispersed cuts, and gap cuts. Variation among treatment replicates was highest in gap and clear-cut treatments, intermediate in dispersed cuts and lowest in uncut stands (Table 1.10). Resemblance was high between clear-cuts and gaps cuts, which had average Bray-

Curtis distance between treatments (22.3% dissimilar) equivalent to the distance within treatments (22.1 and 22.4% dissimilar respectively).

Table 1.9 PERMANOVA pair-wise tests among mixed stand treatments

Groups	df	t	P(perm)	P(MC)
Control x Cc*	5	2.3264	0.0984	0.0339*
Control x Dispersed	5	1.3818	0.0994	0.1818
Control x Gap*	5	2.1754	0.0936	0.0276*
Cc x Dispersed	5	1.6047	0.1037	0.1107
Cc x Gap	5	1.0306	0.5002	0.3916
Dispersed x Gap	5	1.1198	0.3021	0.3255

* indicates significant difference between groups uncorrected for multiple comparisons

Table 1.10 Average Bray-Curtis distance within/between mixed stand treatments

Treatment	Control	Cc	Dispersed	Gap
Control	**11.688**			
Cc	27.482	**22.120**		
Dispersed	17.225	24.701	**17.884**	
Gap	26.368	22.269	20.530	**22.384**

The oldest stands in the study had only two treatments for a simple test (controls and clear-cuts) which were found to host significantly different carabid assemblages (t=2.511, P(permutation) = 0.0984, P(Monte-Carlo)= 0.0185).

1.3.4 Multivariate regression tree community model

The multivariate regression tree model (Figure 1.4) explains 67.98% of the variance in carabid composition using silvicultural treatments and forest cover types. The first split dividing aspen prescribed burns and whole tree harvest from all other treatments and forest types explains 27.36% of the community variance. The second split explains 11.64% of community variance by separating uncut stands and dispersed partial-cuts from gap-cuts, clear-cuts and natural fire. The third split explains 8.18% of carabid variance by differences between prescribed burns and whole tree harvest. The fourth and fifth splits each explain 5.35% of the community

variance and explain differences between beetle communities in pure aspen or mixed and balsam fir-birch closed canopy stands; and mixed forest gap or clear-cuts versus aspen and balsam fir-birch clear-cuts or wildfire respectively. The following split separates mixed uncut stands from balsam fir-birch stands explaining 3.83% of community variation. The final two splits explaining 3.19% and 3.08% of the community variation respectively first separate natural fire from clear-cuts and then the balsam fir-birch and aspen clear-cuts themselves. The table in Appendix B summarizes model parameters influenced by each split of the MRT.

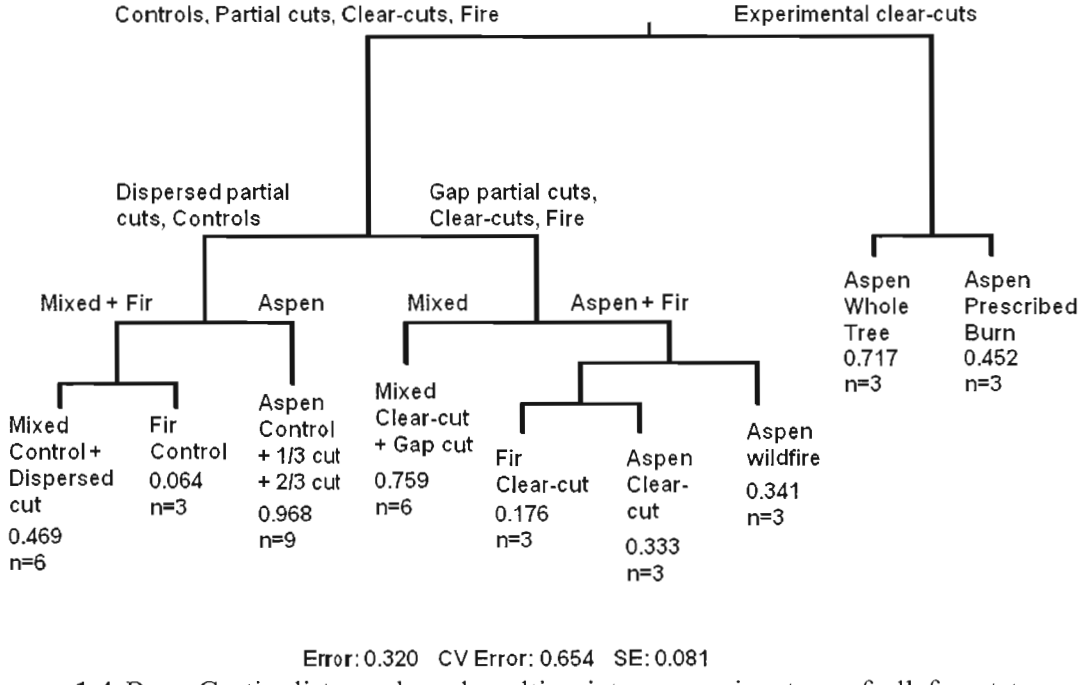


Figure 1.4 Bray Curtis distance-based multivariate regression tree of all forest types and treatments summarizing results of PERMANOVA analyses. Cross-validated (CV Error) refers to the predictive power of the model. The number below each terminal node is the average sum of squares of Bray-Curtis distance. "n" is the number of sample replicates in each terminal node.

1.3.5 Treatment and cover type indicators

Species affinities for specific treatment groupings as defined by indicator analysis of the MRT terminal nodes are summarized in Table 1.11. Five species: *Harpalus laticeps* (LeConte), *Harpalus egregious* (Casey), *Harpalus plenalis* (Casey), *Poecilus lucublandus* (Say), and *Syntomus americanus* (Dejean) were consistently associated with prescribed burn sites. *Pseudamara arenaria* (LeConte) was the only species with an indicator value of 100 and was found exclusively in the three replicates of balsam fir-birch forest clear-cuts. While no species showed affinities for clear-cuts in aspen stands, clear-cuts and gap-cuts within mixed stands were preferred by *Sphaeroderus stenostomus* (Dejean) and *Badister obtustus* (LeConte). Three species had affinities for uncut mixed and balsam fir-birch forests: *Pterostichus punctatissimus* (Randall), *Platynus decentis* (Say), and *Pterostichus adstrictus* (Eschscholtz). Five species preferred wildfire sites: *Calathus ingratus* (Dejean), *Clivina impressifrons* (LeConte), *Agonum retractum* (LeConte), *Platynus mannerheimii* (Dejean), and *Pterostichus melanarius* (Illiger).

Table 1.11 Carabid indicators of forest cover and treatments

Species	Indic. value	Relative Abund. (%)	Relative Freq. (%)	P	Treatment affinity
P. adstrictus (Eschscholtz)	61	60.6	100	0.001	Fir & mixed cont.
P. punctatissimus (Randall)	63	62.9	100	0.009	Fir & mixed cont.
P. decentis (Say)	52	52.4	100	0.001	Fir & mixed cont.
P. arenaria (LeConte)	100	100	100	0.001	Fir clear-cut
B. lugubris (LeConte)	47	46.9	100	0.010	Fir clear-cut
S. stenostomus (Dejean)	64	63.7	100	0.001	Mixed c-c & gap
B. obtusus (LeConte)	43	51.8	83.3	0.023	Mixed c-c & gap
H. laticeps (LeConte)	88	88.4	100	0.002	Prescribed burn
H. egregious (Casey)	78	77.7	100	0.004	Prescribed burn
P. lucublandus (Say)	68	67.9	100	0.005	Prescribed burn
S.s americanus (Dejean)	44	44.2	100	0.028	Prescribed burn
H. plenalis (Casey)	66	100	66.7	0.001	Prescribed burn
P. mannerheimii (Dejean)	67	100	66.7	0.001	Wildfire
C. ingratus (Dejean)	59	58.9	100	0.001	Wildfire
C. impressifrons (LeConte)	50	75.1	66.7	0.023	Wildfire
P. melanaurius (Illiger)	42	63.0	66.7	0.033	Wildfire
A. retractum (LeConte)	30	30.3	100	0.012	Wildfire

1.4 Discussion:

1.4.1 Synthesis of Results

Using PERMANOVA tests and a MRT model, we were able to define distinct carabid assemblages in control stands, clear-cuts, and within forest types summarizing the changes in carabid species composition in response to management and natural processes. The measures of species richness, relative-abundance, and specific affinities for forest types and treatments are important for interpretation of the community differences portrayed in the MRT model.

For example, carabid assemblages found in whole tree removal and prescribed burn treatments differed from those in uncut stands more than assemblages found in wildfire or any of the other treatments used in the experiment. These differences can be attributed to a combination of low beetle abundance and high catch variability between sites that was unique to these treatments. Prescribed burns were further

differentiated from whole tree removal by the high number of species in relation to the number of individuals collected and a unique set of pyrophyllic beetles found only in this treatment. Beetle assemblages in whole tree harvest were species-poor and had the lowest average catch rates in the SAFE experiment. Studies on fire and salvage logging in western Canada (Koivula and Spence 2006, Cobb et al. 2007) demonstrate that compounded disturbances can promote carabid species richness while reducing abundance, similar to our findings in aspen prescribed burns. Compounded disturbances such as salvage logging and post-clear-cut prescribed burning may increase habitat heterogeneity and promote species diversity for ground beetles by exposing mineral soil through mechanical disturbance, accelerating integration of woody material in the case of salvage harvest, or leaving a mosaic of burned and unburned slash in the case of prescribed fire. In contrast, compounded disturbances that remove habitat heterogeneity such as commercial clear-cuts with mechanical removal of slash (Gunnarsson et al. 2004) have been shown to significantly reduce carabid abundance and species richness, similar to our finding in whole tree harvest sites. These methods homogenize microhabitats for ground beetles, remove sources of shade and water retention, and increase exposure to heat and light. In this environment it is not surprising that beetle abundance was 66% lower than nearby uncut stands and species diversity was 33% lower than adjoining prescribed fire sites.

Differences in relative abundance of forest and open area generalist species (as described by Niemela et al. 1993, Koivula 2001, and Jacobs et al. 2008) were responsible for the MRT split between intact canopy sites (controls and dispersed cuts) and open canopy sites (clear-cuts, wildfire, and gap-cuts). Carabid assemblages associated with specific cover types were responsible for the splits between uncut closed canopy forests; however several of these canopy preferences seem to vary between Eastern (Pearce et al. 2003, our study) and Western Canada (Spence et al. 1996, Work et al. 2004, Jacobs et al. 2008). In western Canada, Work et al. (2004) found *P. pensylvanicus, A. retractum, and P. decentis* to be associated with deciduous

canopies, and Jacobs et al. (2008) classified *P. pensylvanicus, A. retractum,* and *P. foveocollis* as deciduous canopy generalists that peak early in stand succession but are also found in later successional stages. Our study showed deciduous peaks for *A. retractum* and *P. pensylvanicus*, however *P. decentis* and *P. foveocollis* were most abundant in mixed and balsam fir-birch forests. In contrast to the mixed and conifer associations of Work et al. (2004) and forest generalist classification of Jacobs et al. (2008), *C. ingratus* in our study was highly correlated with deciduous forests and was an indicator of deciduous wildfire that maintained intermediate abundance in mixed stands and showed a steep decline in older uncut stands. In Eastern Canada, Pearce et al. (2003) also found distinct communities in pure deciduous and conifer dominated stands, however in mixed jack pine and aspen stands, carabid assemblages were indistinguishable from similarly aged pure aspen stands. This similarity in carabid assemblages between compositionally different but similarly aged stands suggests that time since fire and related accumulation of litter and woody material should be considered along with canopy cover as drivers of carabid assemblage succession.

The dominance of aspen stands by habitat generalists and conifer stands by habitat specialists is likely related to structural and physical changes in the forest floor with increasing stand age. Holliday (1992) speculated that carabid preferences for deciduous or conifer canopies are related to substrate and microhabitat differences that create unique conditions for foraging and oviposition under different canopy types. Higher temperature and moisture variability, seasonally abundant herbaceous plants and seed sources, and fast-decomposing leaf litter in deciduous stands favor generalist predators capable of adapting to multiple food sources. In contrast, older stands characterized by high humidity, moisture retention, reduced temperature extremes, and accumulated litter (Brais et al. 1995) provide more constant conditions for the development of habitat specialists (Franklin and Spies 1991). For carabid predators, this stabilization of conditions is also likely to influence available food sources as the number of saproxylic and mycophagous prey increase with accumulated downed woody material.

The classifications of Niemelä (1993), Spence et al. (1996), Koivula (2001), Klimaszewski et al. (2005) and Jacobs et al. (2008) do not differentiate between open canopy or disturbance specialist carabids by pre-disturbance cover type, however we found consistent differences between species in aspen, mixed, and balsam fir-birch clear-cuts, post-harvest prescribed fire, and whole tree removal treatments. Some of these differences may be attributed to the colonization of disturbed areas by closed-canopy species from surrounding stands (Koivula 2001), or small groups that may have been able to maintain a population within legacy features such as accumulated woody debris and litter from older original stands (Franklin et al. 2000). Previous studies on beetle response to whole tree harvest (Bellocq et al. 2001) and post clear-cut prescribed fire (Beaudry et al. 1997) have shown consistent differences between carabid communities in standard clear-cuts and in treatments that reduce substrate structures such as CWD and litter. Light topsoil preparation (harrowing) has been shown to further reduce the abundance of forest generalists in clear-cuts while favoring open area generalists (Koivula and Niemelä 2003, Klimaszewski et al. 2005, Pihlaja et al. 2006). These assemblage changes imply that residual substrate structure, which varies with stand age and cutting intensity, plays an important role in determining insect communities after clear-cutting.

Contrary to the behavioral classifications mentioned previously, individuals of *P. arenaria* were trapped in each of the three replicates of the balsam fir-birch clear-cuts but not in surrounding forests or other disturbance types. Little is known about the biology of this species (Larochelle and Larivière 2003), so for the moment, one can only speculate about the habitat conditions found in old stand clear-cuts that are responsible for the presence of this species. Some possible explanations might include associations to one or a combination of: raspberry brambles and open canopy (Bertrand 2005), high accumulated woody debris, a thick hummus layer, and reduced competition from closed canopy species. *P. arenaria* is an example of one of many poorly studied rare species with patchy

distribution. Until studies are completed on the unique habitat requirements for each of these species, the only way to ensure their maintenance on the landscape is to retain a variety of forest ages, disturbance types, and their related structures.

Work et al. 2004 and Jacobs et al. (2008) found high carabid species overlap between stands with a conifer component of the canopy (both mixed and conifer dominated), which is similar to the findings of our study in which the three indicators of conifer-component forests: *P. decentis, P. punctatissimus*, and *P. adstrictus* were nearly evenly split between mixed and balsam fir-birch stands.

Variance in carabid assemblages that was not explained by silvicultural treatments or forest cover types may be related to other environmental factors such as inter-annual variation in temperature (Abildsnes and Tømmeros 2000), moisture gradients (Holliday 1992), coarse woody debris (Spence et al. 1996, Niemelä 1997), and litter form and depth (Holliday 1992). In disturbed sites, resource and shelter limitations may also increase the potential for predation and intra-guild competition (Niemelä 1993, Currie et al. 1996).

Discrepancies between PERMANOVA and MRT results

Several notable differences were found between PERMANOVA pair-wise tests for significant community differences and the global MRT model. These differences can be attributed to the way Bray-Curtis distances are used in each method. PERMANOVA tests differences between treatments by comparing the Bray-Curtis distances between replicates of the same treatment to those of other treatments. Because Bray-Curtis dissimilarity was very high between replicates of whole tree removal (43.9%), controlled burns (30.0%), and aspen clear-cuts (32.8%), replicates of these treatments could not be differentiated from other aspen treatments in simple pair-wise comparisons. In contrast, the MRT model simultaneously compared each treatment and forest type based on the minimized sum of squares of

Bray-Curtis dissimilarities. The first split of the model removed the two treatments with the greatest within and among group dissimilarities (whole tree and prescribed fire), meaning that these two treatments were comprised of beetle assemblages that had the least in common with those in all other treatments and forest types. While the MRT model does not provide a traditional p-value to test the components of each community split, the sum of squares method used by the model appears to be more robust to highly variable data by making multiple comparisons to determine group membership. Further emphasis should be placed on the results of the MRT model and global PERMANOVA tests over pair-wise PERMANOVA tests because application of p-value correction for multiple comparisons rendered all but one test (comparing uncut and clear-cut balsam fir-birch stands) not significant.

1.4.2 Contrast between clear-cut, prescribed burn, and wildfire assemblages

In Aspen stands of northern Alberta, Buddle et al. (2006) found carabid species richness to be higher in clear-cut stands than in natural wildfire sites both immediately after and up to 26 years post disturbance. Our results show a similar pattern for aspen clear-cuts and wildfire seven and ten years post disturbance, however prescribed burns had much higher estimated species richness than clear-cutting or wildfire alone. In our study the prescribed burn treatment was expected to best emulate a wildfire beetle community; however the unique assemblage found in this treatment seemed to fall outside of the natural range of diversity between intact aspen forests and recovering natural burn communities. No comparable studies were found in aspen forests; however, Beaudry et al. (1997) noted increased species richness with clear-cut burns (in comparison to clear-cutting or fire alone) in jack pine stands of eastern Ontario. Beaudry et al. (1997) suggested incorporating controlled burn treatments after clear-cut as a way to promote pyrophyllic species, however Wikars (1997) found that one of the most abundant post-fire colonizing carabids *Sericoda quadripunctata* was missing in controlled burn sites that were first subjected to clear-cutting and proposed that low burn-intensities associated with

prescribed burn treatments may not achieve high enough severity for some pyrophyllic species. Including a range of burn intensities in post clear-cut prescribed burns may be one way to better emulate natural fire behavior and meet the habitat requirements of more pyrophyllic species.

High species richness associated with clear-cut burns may be a factor of the compounded effect of the disturbance that recruits: 1) open area generalists found in all stand replacing disturbances (Niemelä et al. 1993, Koivula 2001) ; 2) residual generalist and forest species associated with the intact litter layer and decomposed woody debris that remains immediately following clear-cutting (Koivula and Niemelä 2002); and 3) pyrophyllic species specifically adapted to burned sites (Saint-Germain et al. 2004, 2005). This series of disturbances, at least for the first few years following treatments, can be related to Connell's (1978) theory of intermediate disturbance in which diversity is maximized under a state of moderate (and in our case compounded) disturbance. Huston (1979) further suggests that the high diversity of intermediately disturbed systems under conditions of moderate site productivity and low population densities (as is the case temporarily following prescribed fire) can be explained by reduced competition for resources. The temporary creation of suitable habitat conditions for multiple carabid assemblages without natural population and competition pressures is likely the cause of the observed high species richness in prescribed burn sites. Insect assemblages after natural wildfire would be expected to vary with burn intensity, and if heating were sufficient to remove litter and much of the original downed decayed wood, the community is unlikely to contain residual species from the pre-fire forest type (Beaudry et al. 1997). An example of this was described by Saint-Germain et al. (2005) who found natural fires in black spruce to contain no forest generalist carabids whereas adjacent clear-cut assemblages were dominated by them. Insect assemblages in clear-cuts would be expected to have intermediate species richness between wildfire and prescribed burns because of the high concentrations of open area and residual forest generalists but no pyrophyllic species. Pyrophyllic species were more

abundant in prescribed burns (six and seven years post-treatment) than in natural burns (10 years post-fire) because pyrophyllic carabids tend to be ephemeral and are replaced by open area generalists (Holliday 1984). In our experiment, species composition and abundances in wildfire sites were intermediary between those in uncut deciduous stands and commercial clear-cuts. The overlap in species and abundances between wildfire and undisturbed aspen stands may be a signal of assemblage recovery following natural versus anthropogenic disturbance. Further evidence of assemblage recovery after wildfire comes from the presence of *Platynus mannerheimii* which is considered a sensitive closed-forest species known to persist for only 1-2 years within disturbed sites (Niemelä et al. 2007). Its presence in wildfire sites nine and ten years post disturbance agrees with the findings of Buddle et al. (2006) that suggest some forest species are capable of significant recovery after wildfire in as little as 10-15 years. Wildfire sites were characterized by high carabid abundance and the presence of deciduous forest generalists which distinguished them from harvested sites. This difference may be related to environmental characteristics retained after fire such as large woody debris and snags that are thought to promote recovery of closed canopy species assemblages and are generally rare following commercial clear-cutting (Franklin et al. 2000).

1.4.3 Regional differences in beetle assemblages

When assessing carabids as indicators of boreal forest management, it is important to note that species vary considerably across the mixedwood region of the boreal forest (Pearce and Venier 2006, Work et al. 2008) and as noted previously, even individual species responses are subject to local forest and environmental conditions. Another example of this is illustrated by *P. adstrictus* which is classified as a forest generalist by Lindroth (1961-1969) and was most common after clear-cuts and in moderately disturbed sites in Alberta (Jacobs et al. 2008, Work et al. 2008). However, in our study in western Quebec and in Pearce et al. (2003) in nearby eastern

Ontario, *P. adstrictus* was predominantly associated with intact mixed and old fir forests and was a sensitive indicator of forest disturbance.

Species assemblages also vary between regions. An example of this is the contrast between our results and those of Work et al. (2004) who found carabid species richness to be constant between mixed and conifer-dominated forests of Western Canada. Our findings were similar to those of Paquin and Coderre (1997), also in southwestern Quebec, who noted a reduction in soil macroarthropod richness with time since fire. These regional differences between individual species behaviors and assemblages in forests of eastern and western Canada underscore the importance of regional indicator inventories such as the work of Paquin and Dupérré (2001) in Southwestern Quebec, Bertrand (2005) in Northwestern New Brunswick, Work et al. (2004) in Northern Alberta, and Gandhi et al. (2005) in Minnesota, USA. Under management, these differences further emphasize the importance of documenting regional variability among indicator responses. Simberloff (2001) and Pearce and Venier (2006) lend support to this point by stating that adapting management prescriptions to local conditions through experimentation at local scale is the only way to establish appropriate indicators of biodiversity response.

1.4.4 Management effects on ground beetle assemblages

Partial cutting effects on beetles

Similarity of carabid communities between dispersed partial cuts and uncut stands in aspen and mixed forests at SAFE agree with the findings of Moore et al. (2004), Peck and Niwa (2005), and Huber et al. (2005), although Vance and Nol (2003) noted in their study that some sensitive forest species were displaced in the short term. Dispersed partial cutting at a level of up to 66% stem removal in aspen stands and 40% stem removal in mixed stands at SAFE seems to maintain beetle assemblages similar to uncut stands 7-years post treatment.

Gap size and age may be important factors determining the effects of gap-cutting on carabid assemblages. In yellow birch-balsam fir forests (Klimaszewski et

al. 2005) and Norway spruce forests (Koivula et al. 2002), small gap cuts up to three times the size of those used in the SAFE experiment contained carabid assemblages that were intermediary between clear-cuts and control stands and were capable of retaining many forest species. In contrast, the present study found carabid assemblages in mixedwood gap cuts to be indistinguishable from those in clear-cuts seven years post treatment. Ulyshen et al. (2006) discussed the importance of gap age in determining carabid responses and noted that the centers of old gaps (seven years post treatment) lacked the forest species that had been found there one-year after treatment. Based on these findings, Matveinen-Huju (2007) suggested that the conclusion of Koivula et al. (2002), which used results from one and two year-old gaps, may have been premature. The same argument can be made for the findings of Klimaszewski et al. (2005), which were also based on collections one and two years post disturbance. A consensus on the long-term effects of gap-cutting on carabid assemblages in multiple forest types has not been reached, though the evidence from Ulyshen et al. (2006) and our study suggest that differences between communities in gaps and surrounding forests persist for at least several years.

Niemelä et al. (2007) proposed gap cutting as an economically and ecologically viable option to maintain carabid assemblage diversity in Finnish forests by concentrating small gap cuts on the periphery of protected forests to assure ample sources of colonizers to repopulate gaps once the stand begins to recover from disturbance. One potential problem with concentrating gap cutting on the periphery of protected areas is the potential for invasion by non-native species (Goβner et al. 2006). While invasive carabids were not found in mixed forest gaps at SAFE, beetle assemblages in this treatment closely resembled those in clear-cuts where *P. melanarius* was present.

1.5 Conclusions

While the lack of beetle assemblage shifts between control, 1/3 cut, and 2/3 cut treatments in aspen stands is consistent with results at the EMEND project in

Alberta (Work personal communication), this result should not be considered an endorsement of indiscriminant use of partial cutting in aspen stands on the grounds of non-significant change in one indicator group. In management decisions it is important to assess the responses of several biodiversity indicators before judging the impacts of a treatment on a natural system. We have already noted the tolerance of deciduous forest-dwelling carabids to disturbance; however the same may not be true for other commonly used bioindicators such as birds, small mammals, lichens, herbaceous plants, and even other arthropods. New research incorporating beetles in the family Staphynilidae as bioindicators have shown this extremely abundant and diverse group to have much greater sensitivity to ecosystem change than carabids (Work personal comm.). Two-thirds partial cutting in aspen stands is designed to accelerate succession towards a mixed stand structure and based on the current regeneration of conifer species in these treatments, the future stand will have little in common with the original control and 1/3 cut treatments (Brais personal comm.). Broad application of 2/3 partial cutting in aspen forests would significantly alter the structure of the landscape and reduce the structural heterogeneity that exists in stands passing through natural succession processes. The intensity of partial-cutting treatments in each region should reflect the natural distribution of stand age classes across the landscape taking care to retain representative proportions of early, middle, and late successional forest types and structures based on the natural fire return interval. Clear-cutting followed by prescribed fire with appropriately placed retention, variable intensity partial cutting, gap-cutting and selective cutting (removing 1/3 to 2/3 of stand basal area), and uncut stands to provide protection to sensitive species and serve as a source for the repopulating of disturbed sites after harvest are components of a comprehensive management plan that can produce wood products while safeguarding ecosystem diversity and related functions. The size requirement for retention patches to protect sensitive species may be as little as 2-10 hectares for ground beetles if appropriate stand age and conditions are incorporated (See Gandhi et al. 2001) whereas, birds, herpeto-fauna, and mammals, may require

interconnected undisturbed forest parcels upwards of 5000 Km^2 or more (Gurd et. al. 2001) containing specific attributes such as old growth forests, wetlands, or other ecologically unique habitats to protect some sensitive species (Hansson and Angelstam 1991, Götmark and Thorell 2003). In setting aside unmanaged parcels, the above estimates should be treated as minimal allowable amounts; the precautionary principle of management suggests that setting aside more unmanaged space is almost always preferred. In the interest of maintaining biodiversity at acceptable levels, it may also be justified to exclude some silvicultural methods such as whole tree harvest which has been shown to severely reduce species abundance and richness and has no natural analog.

Long-term studies on insect recovery after clear-cutting are still needed. While the treatments at SAFE are too recent to answer questions on carabid assemblage recovery over time, early evidence in aspen forests (Buddle et al. 2006) and Norway spruce stands (Koivula et al. 2002) suggest a convergence toward pre-disturbance conditions 30-60 years post-clear-cut, however Desender et al. (1999) warn that recovery of carabid fauna after repeated intensive disturbance may take hundreds of years. Continued studies monitoring the long-term effects of silvicultural treatments on biodiversity in all forest types subjected to harvesting pressures is the only way to assess the long-term impacts of harvesting on ecosystems. Silvicultural experiments and long-term monitoring projects are a relatively new idea with much room for improvement and expansion. The silvicultural experiments conducted at SAFE and elsewhere in Canada are still young and are some of the first projects designed for long-term forest ecosystem monitoring. Silviculture experiments in the United States are concentrated in the Pacific Northwest and have also only begun in the last 15-20 years. These projects address only a tiny fraction of the forest currently being harvested across the continent. The establishment of more long-term monitoring projects should be paramount in the minds of industry and federal forest regulators to assure that the best possible science is used in managing this crucial resource.

The continued use of clear-cutting to emulate wildfire in the NDBM model (Bergeron and Harvey 1997, Harvey et al. 2002 and Bergeron et al. 2002) is convenient for the forest industry; however the resulting stand structure and species assemblages have little in common with naturally burned sites. Early results from aspen forests suggest some convergence between insect assemblages from clear-cuts and wildfire after 28-29 years (Buddle et al. 2006), however long-term studies in a variety of forest types are needed. McRae et al. (2001) identify several aspects of natural fire such as high CWD inputs, variable burn intensities, and green islands (Gandhi et al. 2004) that are difficult to emulate with clear-cut silviculture. In light of these concerns, it seems prudent to invest more time and effort into developing new silvicultural techniques that better emulate the behavior of fire, taking into account aspect, drainage, weather patterns, and structural components to leave behind a heterogeneous landscape with standing snags, variable retention including green islands in hydric sites (Gandhi et al. 2001), a variety of surface substrate treatments, and abundant woody debris.

In much of the Canadian Boreal Shield, aspen, young mixedwood, and balsam fir-birch stands are essentially the same forest at different moments along the cycle of succession and disturbance. Insect community diversity within this system can be viewed not as a geographic or spatial distribution but as a temporal snapshot of species adapted to a certain stage of forest succession at a specific time. From a management standpoint this emphasizes the importance of mixed forest ages and stand compositions to maintain the natural range of diversity. Current even-aged management limits insect community diversity and likely similarly affects other important ecosystem contributors. Beetle assemblage shifts along disturbance and successional gradients are an important indication of faunal community tolerance to silviculture and are useful for evaluating management models. Long-term studies and continued experimentation to adapt ecosystem-based management to all natural forest types that are currently producing timber are essential for developing informed sound

management practices that preserve the integrity of forest resources, forest ecosystems, and the forest industry.

CHAPITRE II

INFLUENCE OF RESIDUAL COARSE WOODY MATERIAL ON GROUND BEETLES (COLEOPTERA: CARABIDAE) FOLLOWING CLEAR-CUT

Le présent chapitre est en préparation pour être soumis à une revue. Les auteurs seront Christopher D. O'Connor, Timothy T. Work, et Suzanne Brais.

2.1 Introduction

Disturbance severity and residual structure play an important role in determining species composition and rate of ecosystem recovery following a stand replacing event (Halpern and Franklin 1990, Turner et al. 1998). Immediately following commercial clear-cutting in boreal forests, ground beetle species assemblages are comprised of a mixture of forest species with associations to pre-disturbance conditions and open area species promoted by the removal of the closed canopy (Niemelä et al. 1993, Niemelä 1997, Koivula 2002, Koivula et al. 2002, Pearce et al. 2003, Buddle et al. 2006). In the previous chapter, clear-cut operations yielded distinct ground beetle assemblages within each successional stage of the boreal mixedwood forest. The methods used to harvest trees were similar in each successional stage, however residual stand features such as volume and decay stages

of coarse woody material (CWM) remaining after harvest varied considerably with stand age and species composition.

Studies of CWM dynamics in the boreal forest of Eastern Canada (Stuartevant et al. 1997, Hély et al. 2000, and Brais et al. 2005) suggest that CWM volume follows a "u-shaped" accumulation curve with time, similar to the trend seen in western forests (Harmon et al. 1986, Spies et al. 1988). Immediately following stand-replacing fire, CWM volume is high as dead and dying snags are integrated into the forest substrate. As early seral species form a new canopy, CWM inputs are greatly reduced and decomposition surpasses accumulation resulting in a trough in the CWM volume curve. With eventual senescence of early seral species, inputs of CWM begin to increase and continue to accumulate through mixedwood and eventual conifer domination, reaching a plateau in old-growth stands (Stuartevant et al. 1997).

Coarse woody material is an important component of forested ecosystems that maintains a variety of sensitive saproxylic animals and fungi and their related ecosystem functions. Management activities that alter CWM dynamics in forested systems have been shown to reduce the abundance and diversity of saproxylic species, and in the case of Fennoscandia, even lead to the red-listing of endangered organisms dependent on large-diameter coarse woody material (Martikainen et al. 2000, Siitonen et al. 2001, Kouki et al. 2001). Gibb et al. (2006) found that artificial augmentation of CWM in clear-cuts maintained some saproxylic species for the first few years following treatment; however they recommended further study on the long-term potential for CWM augmentation to preserve saproxylic insect communities.

Work et al. (2004, 2008) and Spence et al. 1996 identify CWM as an important factor promoting ground beetle diversity and abundance in old growth forests, however the role of CWM in shaping carabid assemblages after canopy removal remains largely untested. CWM in disturbed areas may protect sensitive species by retaining moisture (Harmon et al. 1986, Brais et al. 2005), providing food sources and refuge from predation (Franklin et al. 2000), and providing conditions for reproduction and overwintering (Goulet 1974). Pearce et al. (2003) noted positive

correlations between volume of CWM and several carabid species in clear-cuts though similar correlations were not found in uncut stands. They hypothesized that CWM volume may not be a limiting factor for forest species in unmanaged mature forests but becomes a limiting factor after canopy removal when the understory is exposed to increased extremes of temperature, light, and desiccation.

To characterize the associations between carabid species found in clear-cuts and residual CWM, we conducted a study of ground beetle abundance and species composition six and seven years post harvest in a series of clear-cut and uncut forests using a fully replicated randomized block design. The variation in CWM volume and decay class distributions by forest type represented ecologically relevant conditions found in natural and commercially clear-cut aspen, mixedwood, and conifer-dominated stand compositions. Other factors such as substrate moisture and temperature, natural regeneration, and accumulated litter were considered autocorrelated with CWM volume and were not examined individually.

2.1.1 Hypotheses:

We used carabid species' associations to volume and decay classes of woody material to assess the role of residual structure in retaining closed-canopy beetle species in clear-cuts. We first examined the impact of harvesting on volume and decay classes of CWM and then compared beetle species associations to CWM in uncut and clear-cut stands to assess the importance of retained CWM following canopy removal.

Volume of CWM following harvest was expected to mirror CWM dynamics in uncut stands where total volume is lowest in stands previously dominated by mature aspen and increases with stand age and relative conifer component (H1). Residual CWM decay classes were also expected to vary with stand composition and age. Inputs of fine woody debris (branches and tree tops) created by harvesting were expected to have the greatest effect on total CWM in aspen stands where CWM volumes were expected to be low and the least effect on total volume of CWM in

mixed or conifer-dominated clear-cuts where volume of residual CWM was expected to be higher.

If CWM is capable of lifeboating sensitive forest species in clear-cuts by creating conditions similar to those found in an enclosed forest, we would expect an increase in closed canopy species with volume of advanced decay class CWM (retained from pre-harvest conditions) (H2). Conversely, clear-cuts in which CWM volume is low relative to uncut stands or is limited to early decay classes (small-diameter CWM created during harvest) would be expected to host few if any sensitive closed canopy species.

2.2 Study Design

2.2.1 Study Site

Clear-cuts were part of the SAFE Project located in the Lake Duparquet research and teaching forest in the Abitibi region of western Québec (48° 86'-48° 32' N, 79° 19'-79° 30' W, Brais et al. 2004b). The replicated experimental design of SAFE is detailed in chapter one and in Brais et al. (2004b) and includes three replicated blocks of each treatment in aspen, mixed, and balsam fir-paper birch forest types. Aspen clear-cuts were conducted over the winter of 1998-1999 in stands that dated from the last stand replacing fire in 1923. Mixed stands were cut over the winter of 2000-2001 and were composed of an aspen and mixed conifer dominated canopy with abundant conifer understory dating from a fire in 1910 (Dansereau and Bergeron 1993). Balsam fir-birch clear-cuts were conducted over the winter of 1999-2000 in a stand that dated from a fire in 1760. This forest type has undergone several outbreaks of spruce budworm (*Choristoneura fumiferana* Clem.), the most recent between 1970 and 1984, which killed off the mature balsam fir component of the canopy and augmented inputs of CWM (Bergeron et al. 1995).

2.2.2 Insect sampling

We used ten pitfall traps in each replicate of aspen, mixed, and balsam fir-paper birch clear-cuts (See Appendix A for detailed experiment and sampling design). Trapping was conducted over two consecutive summers in each forest type starting with continuous sampling of aspen clear-cuts between 8 May and 26 August 2004. The following year sampling was expanded to aspen, mixed and balsam fir-birch clear-cuts between 28 May and 8 September 2005, and continued in mixed and balsam fir-birch between 6 May and 23 September 2006.

2.2.3 Coarse woody material sampling

Over the summers of 2004 and 2005, measurements were taken along line-intercept sampling transects 18 m in length along the north to south axis bisecting the centers of each of the five permanent sampling plots within clear-cut and uncut forest replicates. The CWM sampling protocols and volume calculations follow Van Wagner (1982) and recorded the diameter, species and decay class of each log greater than 2.5 cm diameter crossing the transect. Estimated volume of CWM per hectare used the average volume for each of the fifteen transects per treatment (five transects in each of three treatment replicates). Definitions of CWM decomposition classes follow Daniels et al. (1997) using a scale from one to five for least to most decayed respectively. For analysis, decomposition classes were condensed to early (stages one and two), intermediate (stage three), and advanced (stages four and five) decay following Brais et al. (2005).

2.3 Analytical Methods

We compared the volume of CWM by decay class (early, intermediate and advanced) in clear-cut and uncut stands of each cover type, to determine the effects of

clear-cutting and stand composition on CWM dynamics using permutation-based multivariate analysis of variance (PERMANOVA) (Anderson 2001). Tests were run with PERMANOVA version 1.6 (Anderson 2005) using 4999 unrestricted permutations of a Bray-Curtis distance matrix of CWM volume (m^3/Ha) by decay class and cover type. Comparisons were made by treatment (CWM volume difference between cut and uncut stands of the same forest type), forest type (CWM volume differences by tree species composition), and treatment crossed with forest type. Statistical tests were deemed significant at a confidence level (p-value) of $X < 0.05$.

Carabid catch rates were standardized by pooling trapping totals from the ten traps per replicate and dividing by the pooled trap days corrected for disturbance or interference with trapping efficiency as described in chapter one. Catch rates of carabid species in clear-cut and uncut treatments (Appendix D.5) were regressed separately against the average volume of CWM in each decay class and summed across decay classes to determine individual species influenced by residual woody debris in each treatment. Linear regression of individual species used untransformed species daily catch rates and CWM volume measurements in the "lm" function of the "stats" package in the R statistical computing environment version 2.7.1 (R Development Core Team 2008). Linear regressions were not forced through the intercept because the required assumption of zero carabid abundance at zero CWM was not met.

Redundancy analysis (RDA) was used to determine the amount of variance in carabid species assemblages from different forest types that could be attributed to CWM based on the linear regression relationships found between individual species and CWM volume. Prior to model selection, carabid catch rates were converted to Hellinger distance using the "decostand" function of the VEGAN package in R. Legendre and Gallagher (2001) recommend using a Hellinger-distance species matrix in canonical analyses because it was found to be more tolerant of zero-inflated data than other metric distance measures. The carabid species matrix included 21 species

occurring in both clear-cut and uncut treatments. Model selection was based on beetle correlation to volume of early, intermediate, and advanced decay class CWM and total volume of CWM. Constrained axes were selected using the VEGAN package "step" function forward selection procedure guided by Akaike information criterion (AIC) and subject to permutation tests of computed F-statistics as recommended to by Legendre and Legendre (1998) and Oksanen (2008). The selected model was significant at a level of $p< 0.02$ and was limited to volume of intermediate and advanced decay class CWM. Site replicates (forest types) were projected in relation to axis one and two of the RDA to aid with interpretation of interactions between carabid species and CWM biplot scores.

Species catch rates were plotted against the gradients of summed CWM to determine if species responses met the linear distribution assumption required for principal coordinates eigenvector-based correspondence analysis (see Appendix D figures D.1-D.4). The grouped plot of species abundance by CWM volume was limited to the eight most abundant species for clarity. Linear fitted models of carabid abundance to CWM volume consistently produced higher R^2 values than quadratic (unimodal distribution) models and were the only model type to significantly correlate abundance with CWM volume ($p<0.05$). From an ecological perspective, species dependent on CWM would be expected to increase in abundance with CWM volume until a saturation point which may or may not be reached under the experimental conditions provided.

2.4 Results

2.4.1 CWM volume by decay class and forest type

Using PERMANOVA tests we found significant differences in CWM volume between clear-cuts and uncut forests ($p=0.007$), between forest cover types ($p=0.0002$), and among controls and clear-cuts of the same cover type ($p=0.0194$) (Table 2.1). These differences are illustrated in figure 2.1 comparing CWM volume by forest cover and decay class in clear-cut and uncut stands.

Table 2.1 Permutational multivariate ANOVA of the effects of harvesting treatment (2 levels) and cover type (3 levels) on CWM volume (3 decay classifications).

Test	df	SS	MS	F	P(perm)	P(MC)
Treatment	1	2767.4909	2767.4909	5.7519	0.0052	0.0072**
Forest type	2	6367.8914	3183.9457	6.6175	0.0004	0.0002**
Trtmnt. X For.	2	3254.0243	1627.0122	3.3816	0.0192	0.0194**
Residual	12	5773.6990	481.1416			
Total	17	18163.1056				

** Denotes significant difference corrected for multiple comparisons

Summed CWM volume in clear-cuts ranged from 56.5 m^3/ ha in aspen to 123.1 m^3/ ha in mixed forest. This trend was reversed in uncut stands which ranged from 56.9 m^3/ ha in mixedwood forest to 114.7 m^3/ ha in aspen stands (Figure 2.1). In uncut aspen stands the abundant CWM was dominated by advanced decay classes, however in aspen clear-cuts, total CWM was reduced by 51% and was composed primarily of intermediate decay stages. In mixedwood stands intermediate decay class CWM was dominant regardless of treatment, however a major shift occurred between uncut and clear-cut CWM volume. Total volume of CWM in clear-cuts was more than double that in control stands, switching from the lowest values of any forest type in control stands, to the highest values recorded following cutting treatments. The average volumes and allocations of CWM in older balsam fir-birch stands were similar in uncut and clear-cut treatments though variation between replicates was higher in uncut stands. These older stands consistently contained the highest concentrations of CWM in advanced stages of decay, though uncut aspen stands also contained considerable amounts of highly decayed CWM (Figure 2.1).

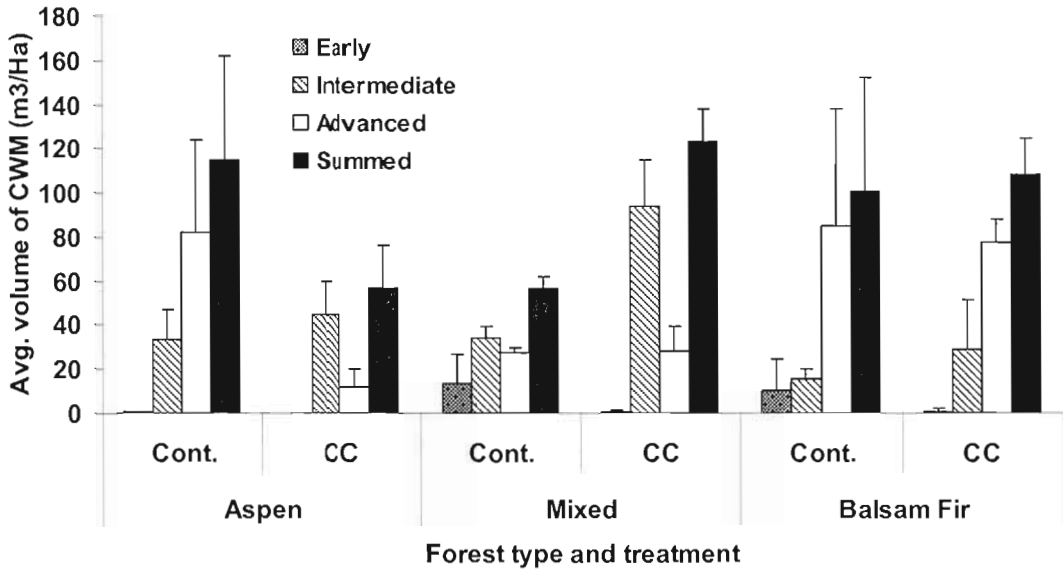


Figure 2.1 Volume and decay classes of woody material in controls and clear-cuts of each forest type. Error bars are one standard deviation.

2.4.2 Species associations to CWM in clear-cut and uncut stands

Linear regression of carabid species on woody material volume by decay class in clear-cuts yielded six species with significant correlations to CWM ($p<0.05$) and four species with marginally significant correlations ($p<0.10$) (Table 2.2). Closed canopy species *Cymindis cribricollis* (Dejean), *Pterostichus coracinus* (Newman), *Pterostichus pensylvanicus* (LeConte), *Patrobus foveocollis* (Eschscholtz), *Pterostichus punctatissimus* (Randall), and *Sphaeroderus nitidicollis* (Guérin-Méneville) were positively correlated to CWM volume in clear-cuts, as were forest generalists *Sphaeroderus stenostomus* (Dejean), and *Pterostichus adstrictus* (Eschscholtz). Species negatively correlated to CWM volume were disturbed area species *Poecilus lucublandus* (Say), and open habitat generalist *Harpalus herbivagus* (Say). Species classifications are based on habitat descriptions from Lindroth (1969), Niemelä et al. (1993) and Koivula (2001).

Table 2.2 Linear regression of individual carabid catch rates by volume of CWM decay class in clear-cuts

Species	Decay class	Slope	Std. Err.	Intercept	R^2	R^2 adj.	F	df	p-val
C. cribricollis	Inter.	0.0001	0.00002	-0.0016	0.445	0.389	8.005	8	0.018*
P. coracinus	Inter.	0.0040	0.00162	-0.0594	0.376	0.314	6.037	8	0.034*
P. pensylvanicus	Inter.	0.0058	0.00162	0.0324	0.562	0.518	12.837	8	0.005*
S. stenostomus	Inter.	0.0024	0.00093	-0.0633	0.397	0.337	6.582	8	0.028*
P .punctatissimus	Adv.	0.0001	0.00001	-0.0007	0.372	0.282	4.149	8	0.081
P. adstrictus (1)	Adv.	0.0011	0.00948	-0.0142	0.725	0.686	18.46	8	0.004*
H. herbivagus	Sum.	-0.0004	0.00017	0.0548	0.312	0.243	4.526	8	0.059
P. lucublandis	Sum.	-0.0008	0.00038	0.0835	0.285	0.214	3.987	8	0.074
P. adstrictus (2)	Sum.	0.0008	0.00035	-0.0351	0.341	0.275	5.166	8	0.046*
P. foveocollis	Sum.	0.0001	0.00016	-0.0029	0.493	0.442	9.723	8	0.011*
S. nitidicollis	Sum.	0.0012	0.00055	0.0078	0.302	0.232	4.329	8	0.064

Significant correlation ($p<0.05$) noted with *. *P. adstrictus* was correlated with both advanced decay and summed CWM.

Only two species (*Scaphinotus bilobus* Say and *S. nitidicollis*) present in both uncut and clear-cut stands were significantly correlated to CWM volume in uncut stands (Table 2.3). While both of these species were positively correlated with multiple decay classes of CWM in uncut stands, neither is significantly correlated with CWM in clear-cuts. *P. adstrictus* was negatively correlated with early decay classes of CWM under a closed canopy; however the correlations with advanced decay classes noted in clear-cuts were not seen in uncut stands. *P. pensylvanicus* was positively correlated with advanced decay class CWM in uncut stands though the strength of the correlation was weaker than the association with intermediate decay class CWM observed in uncut stands.

Table 2.3 Linear regression of individual carabid catch rates by volume of CWM decay class in uncut stands.

Species	Decay class	Slope	Std. Err.	Intercept	R^2	R^2 adj.	F	df	P-val.
P. adstrictus	Int.	-0.0146	0.00633	0.7902	0.432	0.351	5.330	8	0.0543
S. bilobus(1)	Adv.	0.0002	0.00005	-0.0002	0.599	0.542	10.448	8	0.0144*
S. nitidicollis(1)	Adv.	0.0022	0.00055	0.0986	0.684	0.639	15.159	8	0.0059*
P. pensylvanicus	Adv.	0.0227	0.01088	0.2377	0.384	0.296	4.364	8	0.0751
S. nitidicollis (2)	Adv.	0.0052	0.00159	0.0860	0.605	0.549	10.738	8	0.0135*
S. bilobus(2)	Sum.	0.0001	0.00004	-0.0042	0.566	0.504	9.136	8	0.0193*
S. nitidicollis(3)	Sum.	0.0017	0.00043	0.0401	0.689	0.645	15.531	8	0.0056*

Significant correlation ($p<0.05$) noted with *. *S. bilobus and S. nitidicollis* were correlated with more than one decay classification of CWM.

The RDA of carabid species relationships to CWM (Figure 2.2) explained 18.1% of carabid species variance with volume of CWM in uncut and clear-cut stands. The first axis of the RDA separated carabid species by association with intermediate or advanced decay stages of CWM and explained 10.63% of species variance. The second RDA axis separated species positively or negatively correlated (below and above the axis respectively) to CWM and explained 7.47% of species variance. Species positively correlated to advanced decay class CWM were located in the lower right quadrant of the RDA. Species positively correlated to intermediate stages of CWM are located in the lower left quadrant of the RDA. Species negatively correlated to advanced decay class CWM were located in the upper left quadrant of the RDA. Species negatively correlated to intermediate decay class CWM were located in the upper right quadrant of the RDA. The strength of species associations to CWM was measured by the perpendicular distance from a species point to the biplot arrow of the CWM decay class. For example, *P. adstrictus* was positively correlated with advanced decay CWM and negatively correlated with intermediate decay CWM. The shorter distance from *P. adstrictus* to the advanced decay class biplot indicated a stronger positive correlation to advanced decay CWM than negative correlation to intermediate decay stages (as was noted in the linear regression tables).

Species scores on or above the CWM biplots were most strongly associated with a specific decay class. Species scores occurring between the biplot arrows were associated with more than one class of CWM. The six species most positively associated with advanced decay class CWM (*P. adstrictus*, *S. nitidicollis*, *S. bilobus*, *Calathus ingratus* Dejean, *Trechus crassiscapus* Lindroth, and *A. retractum*) are all forest species. The four species negatively associated with volume of advanced decay CWM were open area generalist species *H. herbivagus* and *P. lucublandis* and aspen forest generalists *Notiophilus aeneus* Herbst and *Clivina impressefrons* LeConte. Of the five species with a strong positive correlation to intermediate decay class CWM, *Cymindis cribricollis* Dejean was the only forest species while *S. stenostomus*, *Pterostichus melanarius* Illiger, *Bembidion praticola* Lindroth, and *S. impunctatus* were open habitat generalists. Species negatively correlated to volume of intermediate decay CWM were closed forest species *P. foveocollis*, *P. punctatissimus*, *P. decentis*, and *P. adstrictus*. RDA parameters and outputs for the two constrained axes are reported in Appendix D.6.

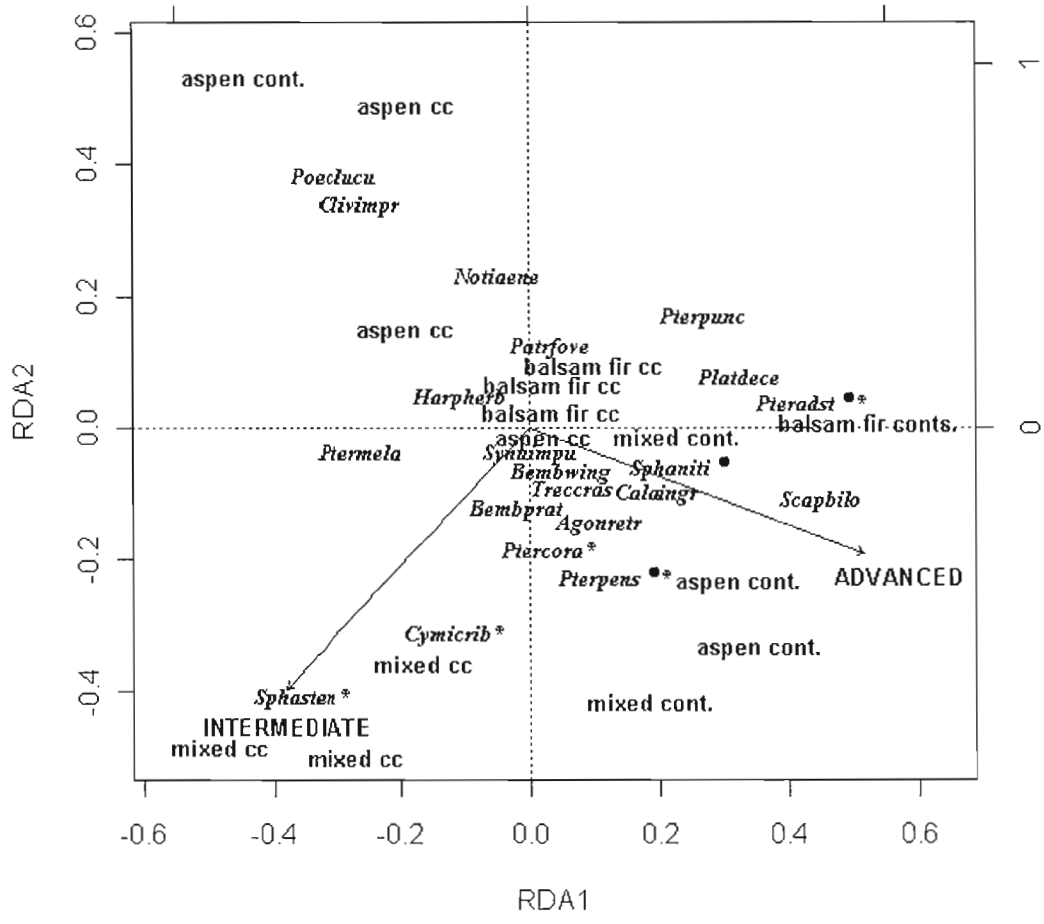


Figure 2.2 Carabid species associations to CWM volume by decay class in clear-cut and uncut stands. Sites are labeled in bold lowercase, environmental variables are at the ends of biplot arrows in bold upper-case and species are bold italics noted with the first four letters of genus and species (ex. *Scaphinotus bilobus* noted as *Scapbilo*). Axes are scaled to the square root of species and site eigenvalues. Asterisks (*) and solid dots (•) indicate species with significant ($p<0.05$) associations to CWM in intermediate and advanced decay stages respectively.

An RDA of clear-cut only sites using the same 21 species co-occurring in uncut and clear-cut stands is detailed in figure 2.3. The second analysis explained 32.1% of the variation in carabid species using the same intermediate and advanced decay classes of CWM but does not include comparisons to uncut stands. With the exceptions of *P. pensylvanicus* switching associations from advanced to intermediate decay class CWM and *S. bilobus* losing its association to advanced decay CWM,

species associations to intermediate and advanced decay stage CWM were consistent between the two analyses. Axis one of the clear-cut only RDA explained 19.1% of species variance by separating positive or negative associations to CWM volume. This was in contrast to the combined clear-cut and uncut stands RDA in which the majority of the variance between species was explained by associations to specific decay classes of CWM. The second RDA axis of the clear-cut only analysis explained 13% of species variance based on preference for intermediate or advanced decay stage CWM. Parameters and outputs for the two constrained axes of the clear-cut only RDA are reported in Appendix D.7.

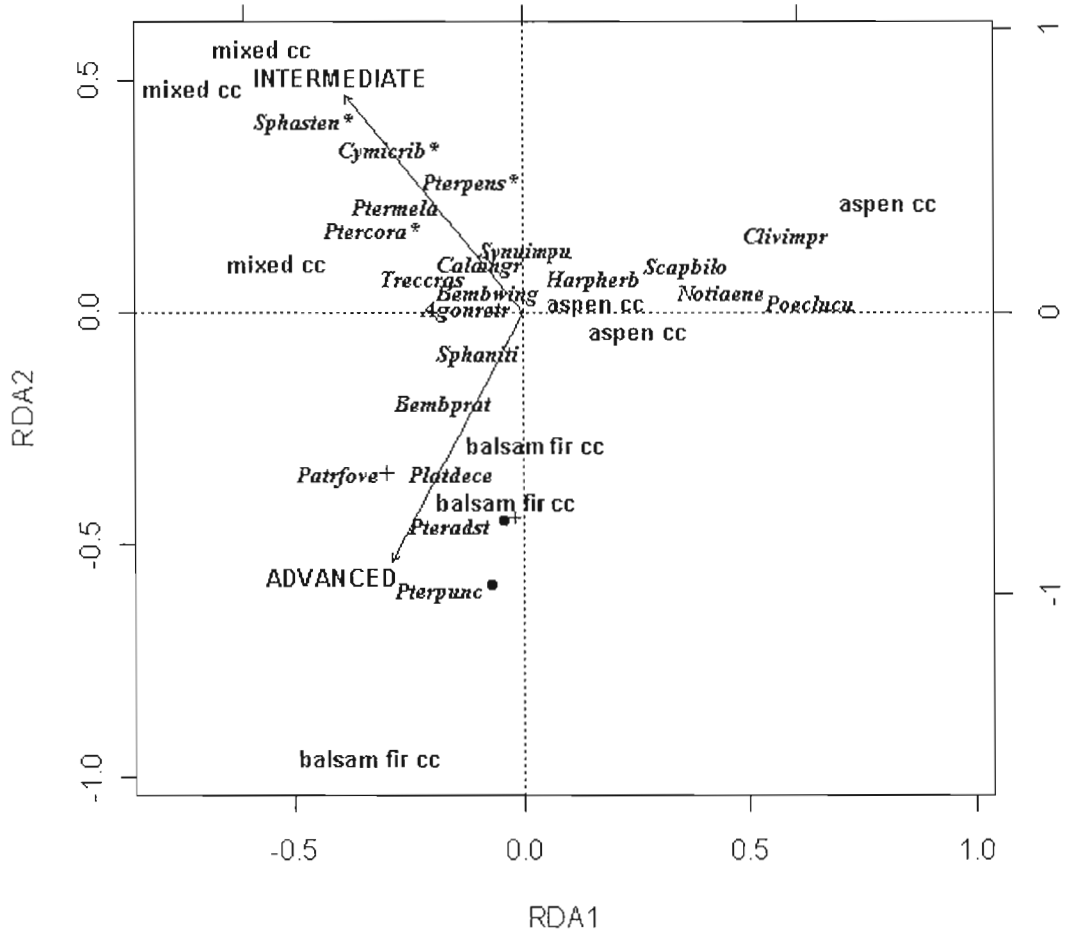


Figure 2.3 Carabid species associations to CWM volume by decay class in clear-cut stands. Sites are labeled in bold lowercase, environmental variables are at the ends of biplot arrows in bold upper-case and species are in bold italics noted with the first four letters of genus and species (ex. *Scaphinotus bilobus* noted as *Scapbilo*). Axes are scaled to the square root of species and site eigenvalues. Asterisks (*), solid dots (•), and plus signs (+) indicate species with significant ($p<0.05$) associations to intermediate, advanced, and summed CWM decay stages respectively.

2.5 Discussion:

2.5.1 Effect of logging on residual CWM

While the volume of advanced decay class CWM was higher than expected in uncut aspen stands, it was drastically reduced in logged aspen stands, making harvesting inputs an important part of residual CWM. Elevated CWM volumes in

uncut aspen stands were likely related to mortality of aspen stems caused by competitive exclusion of shaded trees by the enclosed canopy or the onset of old stem senescence. It is unlikely that residual CWM from the previous forest type was retained after more than 80 years of stand recovery.

Lower than expected volume of CWM in uncut mixed forests may indicate that senesce of the aspen canopy had not yet begun, though a significant increase in CWM inputs would be expected in the near future. The increase in intermediate decay class CWM in mixed stand clear-cuts can be explained by the decay of logging inputs six years after harvest based on the logging slash decay rate observations of Spaulding and Hansbrough (1944). This finding accounts for the general increase in intermediate decay class CWM in clear-cuts of all forest types.

The prevalence of forest and open habitat carabid species with associations to intermediate decay class CWM in clear-cuts implies that the creation and deposition of slash at the time of harvest plays a significant role in determining post-harvest carabid assemblages. Further evidence of logging slash as a resource for carabids is found in Gunnarsson et al. (2004) who noted that residual slash from conifer clear-cuts significantly increased ground beetle abundance and diversity in comparison to stands where slash has been removed.

2.5.2 Influence of CWM on carabid assemblages after disturbance

The prevalence of closed canopy carabid species in clear-cuts with high volume of advanced decay stage CWM and habitat generalists in clear-cuts with high volume of early decay stage CWM suggests that both type and volume of residual woody material play a role in determining species assemblages for several years following disturbance.

The strong correlation between CWM volume and closed forest species *P. coracinus*, *P. foveocollis*, *P. adstrictus*, *C. cribricollis*, and *P. punctatissimus* in clear-cuts and no correlation in uncut stands is consistent with an increased dependence on CWM following canopy removal suggested by Pearce et al. (2003). These species

may be using CWM to persist in "hostile" clear-cut conditions at significantly reduced abundance levels until more favorable conditions develop (ie. development of a closed canopy and renewed deposition of CWM), corroborating the potential of CWM to "life boat" some forest species (Franklin et al. 2000). Similar "life-boating" of closed forest carabid species has been documented for leave-islands (Gandhi et al. 2004, Matveinen-Huju et al. 2006) also containing substantial accumulated CWM.

2.5.3 Beetle response to CWM in clear-cut and uncut stands

In the first RDA analysis explaining carabid associations to CWM in clear-cut and uncut stands, the majority of species variance was explained by preference for specific decay classes of CWM. In the clear-cut only RDA, the majority of species variance was explained by the presence or absence of CWM. The switch from carabid preferences for specific decay classes of CWM in uncut and clear-cut stands to CWM presence or absence in the clear-cuts alone suggests a shift in carabid species associations to CWM following clear-cutting. Species with specific preferences for advanced decay class CWM under a closed canopy may be forced to settle for intermediate decay class CWM following canopy removal in order to maintain a population under sub-optimal conditions. An example of this adaptation behavior is seen with the CWM associations of *P. pensylvanicus* which was the only species strongly correlated to CWM regardless of canopy cover. This species changed associations from highly decayed CWM in uncut stands to intermediate decay stages in clear-cuts. Based on the differences between available CWM in uncut and clear-cut aspen and mixedwood uncut stands where *P. pensylvanicus* was most abundant, the change in CWM association was likely driven more by necessity than preference as the advanced decay classes of CWM abundant in uncut stands were greatly reduced in clear-cuts of these forest types.

S. bilobus and *S. nitidicollis* were strongly associated to CWM volume in uncut stands but seemed to lose this association in clear-cuts, suggesting a change in habitat associations or behavior in disturbed sites. As members of the Cychrine

group of carabids, *S. bilobus*, and *S. nitidicollis* are specialized predators of terrestrial mollusks (Digweed et al. 1993). Clear-cutting may have caused a shift in terrestrial mollusk types from snails in uncut stands to slugs in open clear-cuts (personal observation). It is possible that a change in available food resources is responsible for the inconsistent habitat associations of *S. bilobus* and *S. nitidicollis*, though populations of terrestrial mollusks were not rigorously sampled in this study.

2.5.4 Origins of closed canopy species in clear-cuts

The origins of closed canopy forest species present in balsam fir-birch and mixed clear-cuts can be explained by a combination of two possible scenarios. The species associated with advanced decay stages of CWM in clear-cut forests supports the potential of CWM to "lifeboat" some pre-disturbance forest species, allowing limited reproduction and population maintenance until redevelopment of canopy closure (Franklin et al. 2000, Franklin 2004). In contrast, CWM may simply facilitate the colonization of disturbed areas by forest generalists, serving as a stepping stone from nearby closed canopy stands. In either case, CWM seems to play an important role in increasing the diversity of carabid fauna following harvesting operations and potentially accelerating the recovery of a closed canopy insect assemblage.

The origins of carabid assemblages after clear-cutting could be definitively tested by manipulating CWM volume at variable proximities to closed canopy stands. A clear-cutting experiment incorporating minimal, commercial standard, and augmented volumes of residual CWM in each successional stage, with commercial standard and augmented CWM volumes distributed in two treatments evenly and at variable distances to a closed canopy, would test the origins of closed canopy carabids in clear-cuts as either residual species surviving in CWM or pioneer species migrating via residual slash from nearby forest into the disturbed area.

2.6 Management implications

Several of the closed canopy species present in conifer clear-cuts had strong associations to CWM volume at levels consistent with amounts found in uncut stands. The presence of these species suggests life-boating or stepping stone functions for deadwood that provide a base population for eventual recovery as the canopy reforms. Carabids in deciduous clear-cuts had much less species overlap with those under a closed canopy, suggesting a longer time period is necessary for the reestablishment of forest species in these treatments.

2.6.1 Aspen Stands

Tinker and Knight (2000) and Pedlar et al. (2002) found CWM inputs following natural fire to be two to three fold higher than those in clear-cuts. In young stands (< 80 years) with low residual CWM, cutting and leaving dead or non-marketable stems combined with retention of some large diameter standing trees to provide long-term inputs of CWM may more closely emulate natural forest structure following fire. These practices would promote beetle species associated with CWM and may help to accelerate convergence towards a closed canopy forest beetle assemblage. Combining these practices with limited use of post-cut prescribed burns would also accommodate pyrophyllic species to further increase resemblance to a natural fire beetle assemblage.

2.6.2 Mixedwood and balsam fir stands

In older mixedwood and conifer-dominated stands it may not be necessary to augment preexisting CWM at the time of harvest; however it would still be prudent to retain large diameter snags and other standing trees to serve as future CWM inputs to support saproxylic species recovery. Scarification is one of the site preparation techniques shown to significantly reduce the abundance of several of the same forest species favored by residual CWM (Klimaszewski et al. 2004). The economic

advantages of scarification and related methods should be weighed against the biodiversity costs before being applied.

Clear-cuts with abundant residual CWM have been shown to retain closed canopy species assemblages for several years following disturbance and in the long-term may expedite the recovery of predisturbance insect communities. Management plans that safeguard CWM help to maintain the natural range of species diversity following disturbance and may promote long-term recovery of closed canopy species assemblages.

If our aim is to retain the natural biodiversity of the mixedwood boreal system while producing marketable timber, we must improve harvesting methods to better emulate the complex natural cycles of succession and disturbance. Coarse woody material is one of many important habitat components for forest species; however the management of this resource is still in its infancy. Understanding the role of CWM in supporting healthy ecosystems and buffering against major ecosystem shifts after fire or other stand replacing disturbance will be crucial to the development of long-term forest management methods.

CONCLUSION GÉNÉRALE

Each of the three defined stages of forest succession in the mixedwood boreal zone of Western Québec hosted a distinct carabid assemblage. In order to maintain this natural variation in insect communities, it will be important to maintain a variety of stand ages and compositions representing the natural stages of forest succession.

Residual structure following harvest has a significant influence on carabid beetle species composition and abundance. Coarse woody debris volume and decay class was a strong predictor of the presence of several forest generalist species and may promote the recovery of closed forest beetle communities. The development of harvesting methods than minimize destruction of intact large woody debris or promote the creation of new woody debris inputs may better emulate natural fire and should be considered.

Insect communities after wildfire are different from those in clear-cuts and post-cut prescribed burns. One method to promote pyrophyllic species assemblages associated with natural fire may be to increase the intensity of prescribed burns on a limited scale. Methods such as whole tree removal harvesting that have no natural analogue and severely reduce biodiversity and species abundance should not be utilized in NDBM regimes.

Beetle communities in dispersed partial cuts (removing up to 66% of stand basal area in aspen stands and 40% of stand basal area in mixed stands) resembled those of uncut stands. Continued use of thinning and selective cutting to promote the characteristics of specific canopy types as specified in the NDBM model is supported.

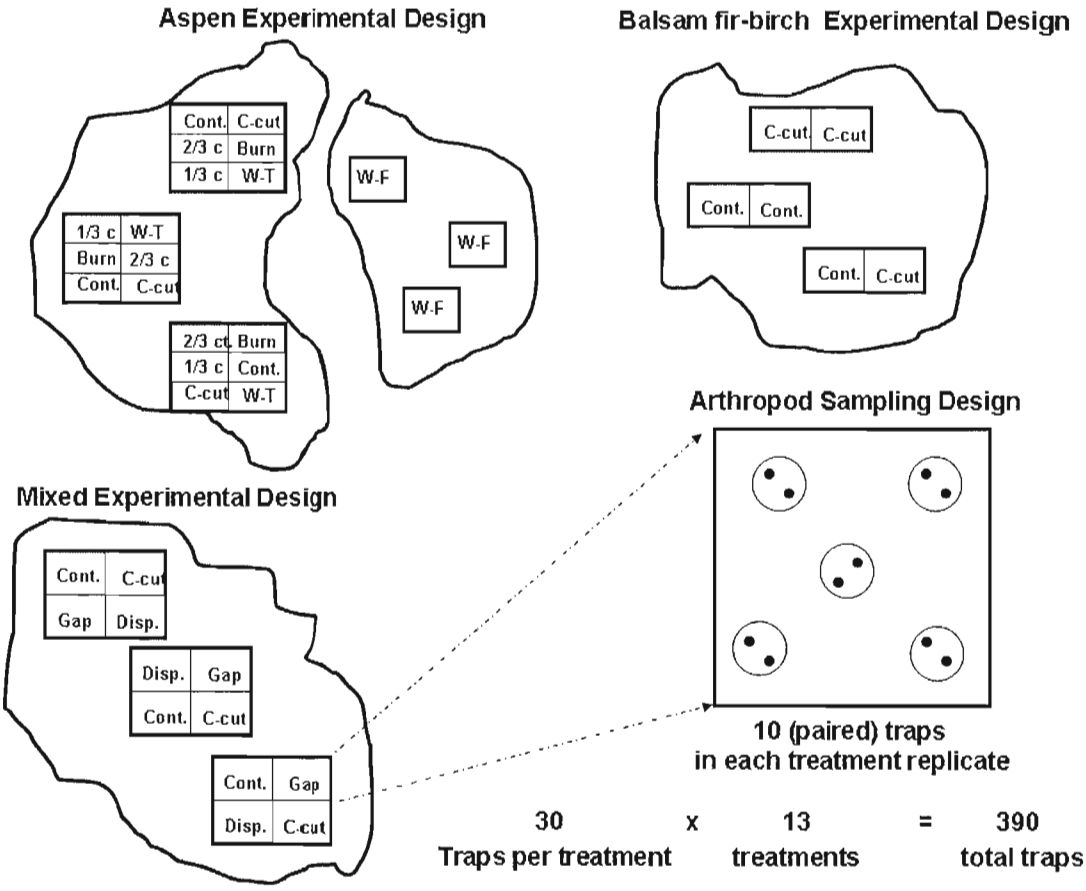
Gap-cutting did not promote carabid species associated with old growth stand structure, instead beetle assemblages in mixedwood gap-cuts more closely resembled those found in clear-cuts. Differing outcomes from gap-cutting in the literature suggest that further study of gap size and shape, as well as scale of the organisms studied will be necessary before the impacts of gap-cutting on biodiversity can be reliably predicted.

There is no one size fits all management prescription for the mixedwood boreal zone of Quebec. Basing management regimes on cycles of natural disturbance is the best practice available to foster the natural range of variation within forest ecosystems. Continued studies of individual charismatic species and sensitive assemblages of species at stand and landscape scales will help fine tune management plans to balance conservation and production goals. The results from current forest management experiments are still preliminary so periodic evaluations of these experiments over the long term will be essential to adapt management practices for the maintenance of biodiversity and ecosystem function.

APPENDICE A

EXPERIMENTAL TREATMENTS AND SAMPLING DESIGN

App. A.1 SAFE Project Randomized Block Sampling Design



Aspen stand treatments: Cont.= control, 1/3c = 1/3 partial cut, 2/3c= 2/3 partial cut, C-cut= clear-cut, Burn= prescribed burn, W-T= whole tree removal, W-F= wildfire. **Mixed stand treatments:** Cont= control, Disp.= 40% dispersed cut, Gap= 40% gap cut, C-cut= clear-cut. **Balsam fir-birch treatments**: Cont.= control, C-cut= clear-cut. Replicated treatments vary from 1-3 hectares.

APPENDICE B
MRT MODEL PARAMETERS AND VARIANCE EXPLAINED

App. B.1 Model parameters explained by carabid community MRT model

MRT split	Complexity parameter	Relative error	Explained variance	Cross Validated error	Std. error
0	0.2735	1.0000	0.0000	1.0559	0.1336
1. Experimental clear-cuts vs. all other treatments	0.1165	0.7265	0.2736	0.9369	0.1001
2. Disp. cuts & Cntrls vs. Gap cuts, Clear-cuts, and Fire	0.0818	0.6100	0.1164	0.8812	0.0957
3. Whole tree harvest vs. Prescribed Burn	0.0535	0.5282	0.0818	0.7773	0.0862
4. Mixed Disp. & Cntrls + Fir Ctrls vs. Aspen Cntrls	0.0535	0.4747	0.0535	0.7611	0.0868
5. Mixed Gap & Clear Cuts vs. Aspen & Fir Clear-cuts & Fire	0.0383	0.4212	0.0535	0.7449	0.0854
6. Mixed Dispersed + Control vs. Fir Control	0.0319	0.3829	0.0383	0.7032	0.0833
7. Wildfire vs. Fir and Aspen Clear-cuts	0.0308	0.3510	0.0319	0.6898	0.0831
8. Fir vs. Aspen Clear-cuts	0.0138	0.3202	0.0308	0.6538	0.0810
Total explained variance			**0.6798**		

APPENDICE C
SPECIES ABUNDANCE BY FOREST TYPE AND TREATMENT

App. C.1 Species abundance by forest type and treatment

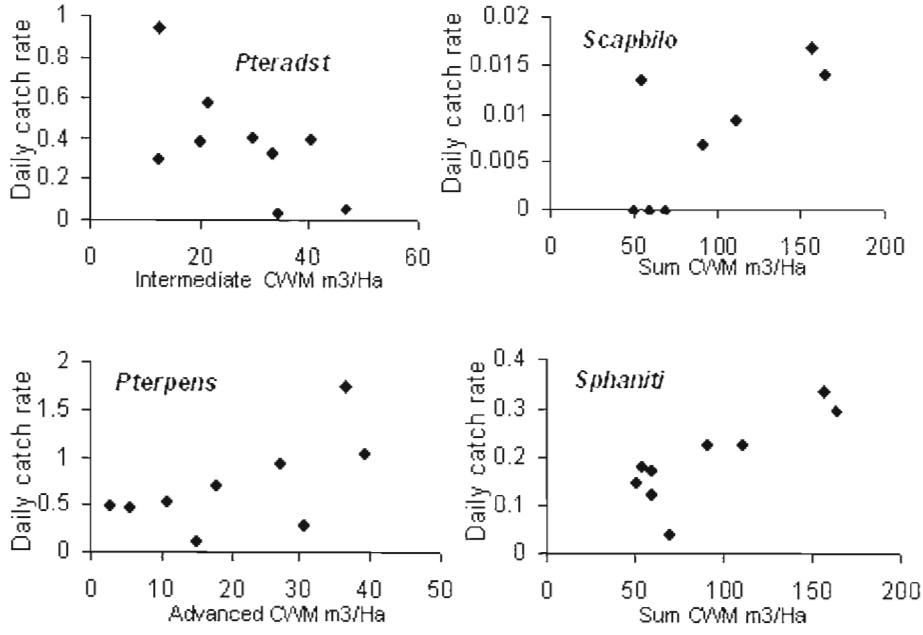
	Aspen							Mixedwood				Balsam fir-birch		
Species	Control	1/3 cut	2/3 cut	Clear cut	Burn	Whole tree	Wild fire	Control	Clear cut	Dispersed cut	Gap cut	Control	Clear cut	Total
Agonum affine		1	1		2					1	1			6
Agonum cupripenne				1	2				1					4
Agonum retractum	179	81	105	170	61	27	324	216	155	228	191	129	133	1999
Agonum tenue								1						1
Amara lunicollis				2	2								2	6
Amara patruelis													3	3
Amara spp 1				1										1
Badister obtusus				1	1	1	2		16		6			27
Bembidion pratincola	1	2	2	1					1		1		2	10
Bembidion wingatei	1	3	2		1		5	2	4	6	2			26
Bradycellus lugubris			1	2	2	1			6		3		10	25
Calathus ingratus	56	10	14	8	4	9	183	57	27	85	27	22	15	517
Calosoma frigidum	1	1	1											3
Carabus maeander				4	24		1		1					30
Chlaenius emarginatus			1	8	7	2								18
Clivina impressefrons	1		1	1			4							7
Cymindis cribricollis	1				1	5	3	2	3	2				17

	Aspen							Mixedwood				Balsam fir-birch		
Species	Control	1/3 cut	2/3 cut	Clear cut	Burn	Whole tree	Wild fire	Control	Clear cut	Dispersed cut	Gap cut	Control	Clear cut	Total
Harpalus amputatus				1										1
Harpalus egregius		1		1	87	9	2			1			2	103
Harpalus erythropus		1												1
Harpalus fulvilabris													1	1
Harpalus herbivagus	5	8	15	31	13	5	19	4	14	9	17	8	12	160
Harpalus honestus							1							1
Harpalus laticeps					16	1								17
Harpalus plenalis					4									4
Harpalus species 1			1											1
Notiophilus aeneus	19	15	10	3	7	2				6	4			66
Olisthopus micans					1									1
Olisthopus parmatus					1				5		1		2	9
Petrobus foveocollis							1	11	1			3	2	18
Platynus decentis	49	49	29	11	6	4	6	164	4	34	13	143	19	531
Platynus mannerheimii							3							3
Poecilus lucublandus	1			8	53	7	1							70
Pseudamara arenaria													19	19
Pterostichus adstrictus	106	32	8	1	15	3	8	268	4	72	6	293	55	871

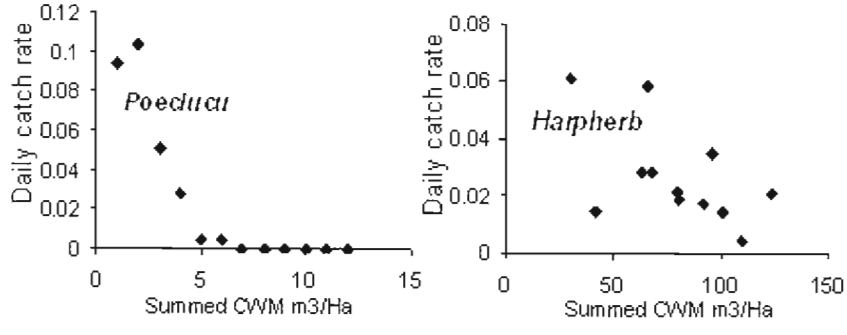
	Aspen							Mixedwood				Balsam fir-birch		
Species	Control	1/3 cut	2/3 cut	Clear cut	Burn	Whole tree	Wild fire	Control	Clear cut	Dispersed cut	Gap cut	Control	Clear cut	Total
Pterostichus coracinus	42	24	22	20	42	9	72	236	291	139	119	134	36	1186
Pterostichus luctuosus				1					1					2
Pterostichus melanarius	6	5	2		2		9		4					28
Pterostichus pensylvanicus	701	520	424	261	99	33	122	404	430	489	267	277	77	4104
Pterostichus punctatissimus								22		9	1	8	1	41
Scaphinotus bilobus	5	3	8	3	1	1	9					8	1	39
Sphaeroderus nitidicollis	120	94	100	77	28	29	19	102	69	117	103	143	91	1092
Sphaeroderus stenostomus							13	67	162	83	190			515
Syntomus americanus				4	11	2			6	1	1			25
Synuchus impunctatus	175	201	193	143	153	94	230	160	194	313	333	88	95	2372
Tachyta angulata					1									1
Trechus crassiscapus	4	2	4	5	3	1	6	18	12	7	6	11	5	84

APPENDICE D

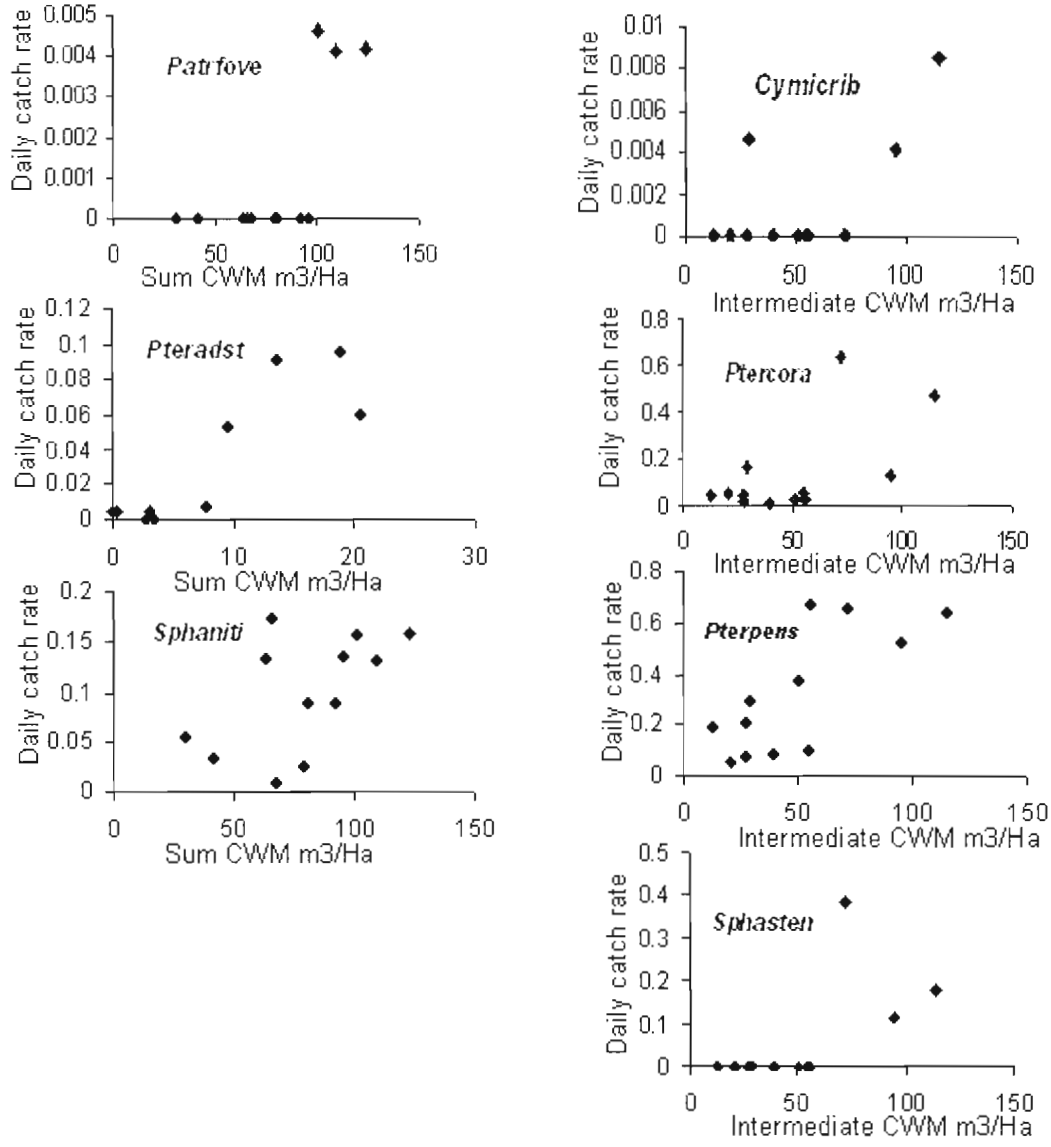
CARABID SPECIES CO-CCURRING IN UNCUT STANDS AND CLEAR-CUTS



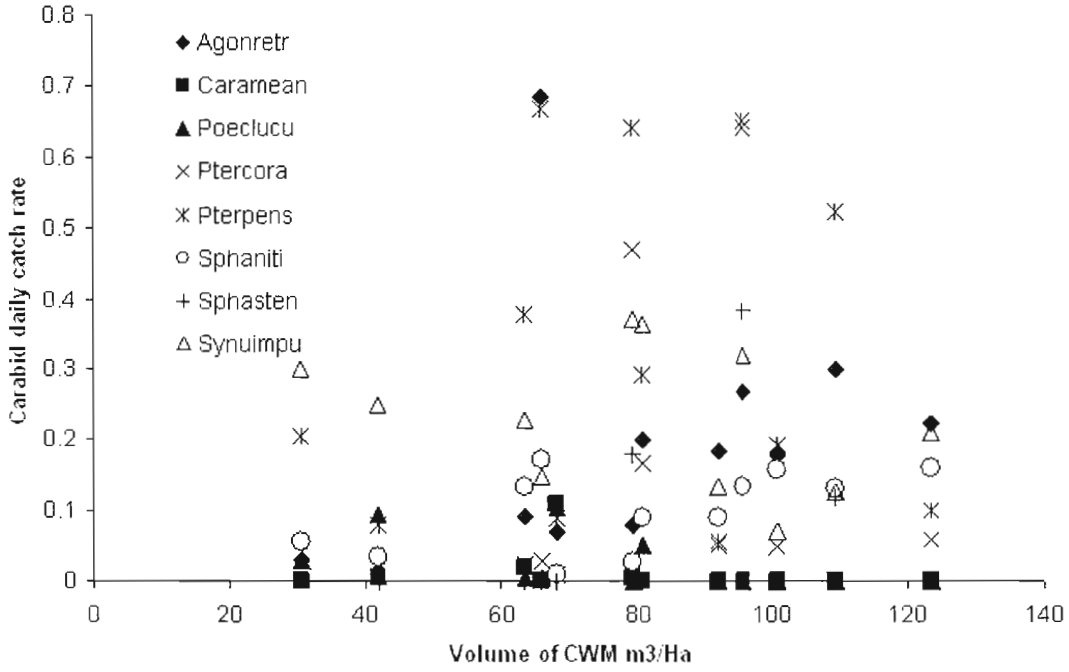
App. D.1 Carabid species correlated with CWM volume in uncut stands. X-axis is volume of CWM in meters cubed per hectare. Y-axis is the corresponding species daily catch rate.



App. D.2 Carabid species with negative correlation to total volume of CWM in clear-cuts. X-axis is CWM volume in meters cubed per hectare. Y-axis is the corresponding species daily catch rate.



App. D.3 Carabid species with positive correlation to volume of summed and decay class 3 CWM in clear-cuts. X-axis is CWM volume in meters cubed per hectare. Y-axis is the corresponding species daily catch rate.



App. D.4. The eight most abundant carabid species found in clear-cuts plotted against summed CWM.

App. D.5 RDA eigenvalues and explained variance for carabid-CWM associations in uncut and clear-cut stands

RDA Axis	1	2	Totals	Variables
Inertia (eigenvalue)	0.057	0.040	0.097	
Variance exp.(%)	10.625	7.473	18.098	
Total inertia			0.535	20
Constrained			0.097	2
Unconstrained			0.438	18

App. D.6 RDA eigenvalues and explained variance for carabid-CWM associations in clear-cuts

RDA Axis	1	2	Totals	Variables
Inertia (eigenvalue)	0.188	0.128	0.316	
Variance exp.(%)	19.141	13.001	32.142	
Total inertia			0.982	20
Constrained			0.316	2
Unconstrained			0.666	18

App. D.7 Abundance and species codes for carabids used in RDA ordinations

		Aspen		Mixedwood		Balsam fir-birch		
Species	Code	Control	Clear-cut	Control	Clear-cut	Control	Clear-cut	Total
Agonum retractum	*Agonretr*	179	170	216	155	129	133	1043
Bembidion pratincola	*Bembprat*	1	1		1		2	5
Bembidion wingatei	*Bembwing*	1		2	4			8
Calathus ingratus	*Calaingr*	56	8	57	27	22	15	189
Clivina impressefrons	*Clivimpr*	1	1					2
Cymindis cribricollis	*Cymicrib*	1		2	3			7
Harpalus herbivagus	*Harpherb*	5	31	4	14	8	12	87
Notiophilus aeneus	*Notiaene*	19	3					29
Patrobus foveocollis	*Patrfove*			11	1	3	2	17
Platynus decentis	*Platdece*	49	11	164	4	143	19	396
Poecilus lucublandus	*Poeclucu*	1	8					62
Pterostichus adstrictus	*Pteradst*	106	1	268	4	293	55	742
Pterostichus coracinus	*Ptercora*	42	20	236	291	134	36	801
Pterostichus melanarius	*Ptermela*	6			4			12
Pterostichus pensylvanicus	*Pterpens*	701	261	404	430	277	77	2249
Pterostichus punctatissimus	*Pterpunc*			22		8	1	31
Scaphinotus bilobus	*Scapbilo*	5	3			8	1	18
Sphaeroderus nitidicollis	*Sphaniti*	120	77	102	69	143	91	630
Sphaeroderus stenostomus	*Sphasten*			67	162			229
Synuchus impunctatus	*Synuimpu*	175	143	160	194	88	95	1008
Trechus crassiscapus	*Treccras*	4	5	18	12	11	5	58

REFERENCES

Abildsnes J. and Tømmeros B.Å. (2000) Impacts of experimental habitat fragmentation on ground beetles (Coleoptera, Carabidae) in a boreal spruce forest. *Annales Zoologici Fennici.* 37: 201–212.

Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology.* 26:32-46.

Anderson, M.J. (2005) User Notes: PERMANOVA permutational multivariate analysis of variance. Dept. of Statistics, University of Auckland.

Angelstam, P., Boutin, S., Schmiegelow, F., Villard, M.-A., Drapeau, P., Host, G., Innes, J., Isachenko, G., Kuuluvainen, T., Mönkkönen, M., Niemelä, J., Niemi, G., Roberge, J.-M., Spence, J. and Stone, D. (2004) Targets for boreal forest biodiversity conservation – a rationale for macroecological research and adaptive management. *Ecological Bulletins.* 51:487–509.

Baker S.C., Richardson, A.M.M., Seeman, O.D., and Barmuta, L.A. (2004) Does clearfell, burn and sow silviculture mimic the effects of wildfire? A field study and review using litter beetles. *Forest Ecology and Management.* 199: 433-448.

Beaudry, S.B., Duchesne, L.C., and Côté, B. (1997) Short-term effects of three forestry practices on carabid assemblages in a jack pine forest. *Canadian Journal of Forest Research.* 27: 2065-2071.

Bellocq, M. I., Smith, S. M., and Doka, M. E. (2001) Short-term effects of harvest technique and mechanical site preparation on arthropod communities in jack pine plantations. *Journal of insect conservation.* 5: 187-196.

Bengston, D. N., (1994) Changing forest values and ecosystem management. *Society and Natural Resources*, 7:515:533.

Bergeron, Y. and Bouchard, A. (1983) use of ecological groups in analysis and classification of plant communities in a section of western Quebec. *Vegetatio.* 56: 45-63.

Bergeron, Y. and Dubuc, M. (1989) Succession in the southern part of the Canadian boreal forest. *Vegetatio.* 79: 51-63.

Bergeron, Y., and Dansereau, P.R. (1993) Predicting the composition of Canadian southern Boreal forests in different fire cycles. *Journal of Vegetation Sci*ence. 4: 827-832.

Bergeron, Y., Leduc, A., Morin, H., and Joyal, C. (1995) Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. *Canadian Journal of Forest Research*. 25 (8): 1375:1384.

Bergeron, Y. and Harvey, B. (1997) Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. *Forest Ecology and Manage*ment. (92): 235-242.

Bergeron, Y., and Leduc, A. (1998) Relationships between Change in Fire Frequency and Mortality Due to Spruce Budworm Outbreak in the Southeastern Canadian Boreal Forest. *Journal of Vegetation Science*. 9(4):493-500.

Bergeron, Y., Harvey, B., Leduc, A., Gauther, S. (1999) Basing forest management on natural disturbance: stand and landscape-level considerations. *Forest Chronology*. 75(1): 49-54.

Bergeron, Y. (2000) Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. *Ecology*. 81: 1500-1516.

Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., and Lesieur, D. (2001) Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. *Canadian Journal of Forest Research*. 31: 384-391.

Bergeron, Y., Leduc, A., Harvey, B, and Gauthier, S. (2002) Natural Fire Regime: A guide for sustainable management of the Canadian boreal forest. *Silva Fenn*ica. 36(1): 81-95

Bertrand, A.S. (2005) Ground beetles (Coleoptera:Carabidae) from Northwestern New Brunswick, Canada: Notes on uncommonly reported species and new provincial records. *Northeastern Naturalist*. 12(3): 287-294.

Bouchard, M., Kneeshaw, D., and Bergeron, Y. (2005) Mortality and stand renewal patterns following the last spruce budworm outbreak in mixed forests of western Québec. *Forest Ecology and Management.* 204 (2005) 297–313.

Bousquet, Y. and Goulet, H. (2008) Canadian Biodiversity Information Facility electronic resources. Ground Beetles of Canada. Government of Canada. http://www.cbif.gc.ca/spp_pages/carabids/phps/s_e.php

Brais, S. Camiré, C., Bergeron, Y., and Paré, D. (1995) Changes in nutrient availability and forest floor characteristics in relation to stand age and forest composition in the southern part of the boreal forest of northwestern Quebec. *Forest Ecology and Management*. 76: 181-189.

Brais, S., Harvey, B.D., Bergeron, Y., Messier, C., Greene, D. Belleau, A.& Paré, D. (2004a) Testing forest ecosystem management in boreal mixedwoods of northwestern Quebec: initial response of aspen stands to different levels of harvesting. *Canadian Journal of Forest Research.* 34(2): 431-446.

Brais, S., Harvey, B.D., Bergeron, Y., Messier, C., Greene, D. Belleau, A.& Paré, D. (2004b) Élaboration d'une approche sylvicole écosystémique pour la forêt boréal mixte. Projet SAFE Rapport Final.

Brais, S. Sadi, F., Bergeron, Y., and Grenier, Y. (2005) Coarse woody debris dynamics in a post-fire jack pine chronosequence and its relation with site productivity. *Forest Ecology and Management*. 220:216-226.

Brais, S., Paré, D., and Lierman, C. (2006) Tree bole mineralization rates of four species of the Canadian eastern boreal forest: implications for nutrient dynamics following stand-replacing disturbances. *Canadian Journal of Forest Research*. 36(9): 2331–2340.

Briand, F. and Cohen, J.E. (1984) Community food webs have scale-invariant structure. *Nature.* 307: 264-267.

Breiman, L., Friedman, J.H., Olshen, R.A., and Stone, C.G.(1984) Classification and regression trees. Wadsworth International Group, Belmont, California, USA.

Buddle, C.M., Langor, D.W., Pohl, G.R.& Spence J.R. (2006) Arthropod responses to harvesting and wildfire: Implications for emulating of natural disturbance in forest management. *Biological Conservation* 128: 346-357.

Cobb, T.P., Langor, D.W., and Spence, J.R. (2007) Biodiversity and multiple disturbances: boreal forest ground beetle (Coleoptera: Carabidae) responses to wildfire, harvesting, and herbicide. *Canadian Journal of Forest Research*. 37 (8): 1310-1323.

Colwell, R.K. & Coddington, J.A. (1994). Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London.* (B) 345: 101-118.

Connell, J.H. (1978) Diversity in Tropical Rain Forests and Coral Reefs. *Science*, New Series. 199 (4335): 1302-1310.

Currie, C.R., Spence, J.R., and Niemelä, J.(1996) Competition, cannibalism and intraguild predation among ground beetles (Coleoptera:Carabidae): A laboratory study. *The Coleopterists Bulletin*. 50(2): 135-148.

Daniels, L.D., Dobry, J., Klinka, K., Feller, M.C., (1997) Determining year of death of logs and snags of Thuja plicata in southwestern coastal British Columbia. *Canadian Journal of Forest Research*. 27: 1132–1141.

Dansereau, P., and Bergeron, Y. (1993) Fire history in the southern boreal forest of northwestern Quebec. *Canadian Journal of Forest Research*. 23:25-32.

De'ath, G. (2002a) Multivariate regression trees: a new technique for modeling species-environment relationships. *Ecology*. 83(4), 2002, pp. 1105–1117.

De'ath, G (2002b) Recursive partitioning and regression trees statistical package version 1.2-4. R project for statistical computing.

Desender, K., Ervynck, A., and Tack, G. (1999) Beetle diversity and historical ecology of woodlands in Flanders. *Belgian Journal of Zoo*logy.129:139-155.

Digweed, S.C. (1993) Selection of terrestrial gastropod prey by Cychrine and Pterostichine ground beetles (Coleoptera: Carabidae). *The Canadian Entomologist*. 125: 463-472.

Dufrêne, M. and Legendre, P. (1997) Species Assemblages abd Indicator Species: The Need for a Flexible Asymmetrical Approach. *Ecological monographs*. 67(3): 345-366.

Frankin, J.F. and Spies, T.A. (1991) Composition, Function, and Structure of Old-growth Douglas-fir Forest. USDA Forest Service PNW Research Station General Technical Report PNW-GTR-285. pp.71-80.

Franklin, J.F., Lindenmayer, D., MacMahon, J.A., McKee, A., Magnuson, J., Perry, D.A., Waide, R., and Foster, D. (2000) Threads of Continuity. *Conservation Biology in Practice*. 1(1): 8-16.

Franklin, J.F. (2004) Comments on draft environmental impact statement for biscuit recover project. University of Washington Department of Forestry. January 20, 2004.

Gandhi, K.J.K., Spence, J.R., Langor, D.W., and Morgantini, L.E. (2001) Fire residuals as habitat reserves for epigaeic beetles (Coleoptera: Carabidae and Staphylinidae). *Biological Conservation.* 102:131–141.

Gandhi, K.J.K., Spence, J.R., Langor, D.W., Morgantini, L.E., and Cryer, K. J. (2004) Harvest retention patches are insufficient as stand analogues of fire residuals for litter-dwelling beetles in northern coniferous forests. *Canadian Journal of Forest Research.* 34: 1319-1331.

Gandhi, K.J.K., Gilmore, D.W., Ball, G.E., Holzenthal, R.W., Katovich, S.A., Koehle, J.J., Larsen, K.J., Mattson, W.J., and Seybold, S.J. (2005) A review of ground beetle species (Coleopter: Carabidae) of Minnesota, United States: New records and range extensions. *Proceedings of the Entomological Society of Washington.* 107 (4): 917-940.

Gibb, H. Pettersson, R.B. Hjältén, Hilszczański, J. Ball, J.P. Johansson, T., Atlegrim, O. and Danell, K. (2006) Conservation-oriented forestry and early successional saproxylic beetles: Responses of functional groups to manipulated dead wood substrates. *Biological Conservation.* 129: 437-450.

Goβner, M., Engel, K., and Ammer, U. (2006) Effects of selection felling and gap felling on forest arthropod communities: a case study in a spruce-beech stand of southern Bavaria. *European Journal of Forest Research.* 125: 345:360.

Gotelli, N.J. (2001). A Primer of Ecology, 3rd edn. Sinauer Associates Inc, Sunderland, MA, U.S.A.

Gotelli, N.J. and Colwell R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters.* 4: 379-391.

Götmark, F. and Thorell, M. (2003) Size of nature reserves: densities of large trees and dead wood indicate high value of small conservation forests in southern Sweden. *Biodiversity and Conservation* 12: 1271–1285.

Goulet, H. (1974) Biology and relationships of Pterostichus adstrictus Eschsholtz and P. pensylvanicus Leconte (Coleoptera: Carabidae). *Quaestiones entomologicae.* 10: 3-33.

Gunnarsson, B., Nittérus, K., and Wirdenäs, P. (2004) Effects of logging residue removal on ground-active beetles in temperate forests. *Forest Ecology and Management.* 201: 229-239.

Gurd, B.D., Nudds, T.D., and Rivard, D.H. (2001) Conservation of Mammals in Eastern North American Wildlife Reserves: How Small Is Too Small? *Conservation Biology*. 15(5): 1355-1363.

Haeussler S. (2004) Une approche écosystémique pour le maintien de la biodiversité végétale des tremblaies de la forêt boréale mixte. Doctoral Thesis. Université du Québec a Montréal. pp 1:209.

Haeussler S. and Bergeron, Y. (2004) Range of variability in boreal aspen plant communities after wildfire and clear-cutting. *Canadian Journal of Forest Research*. 34: 274-288.

Halpern, C.B., and Franklin, J.F. (1990) Physiognomic Development of Pseudotsuga Forests in Relation to Initial Structure and Disturbance Intensity. *Journal of Vegetation Science*. 1(4): 475-482.

Hansson, L. and Angelstam, P. (1991) Landscape ecology as a theoretical basis for nature conservation .*Landscape Ecology*. 5(4): 191-201.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack Jr., and K. W. Cummins (1986) Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecology Research*. 15: 133-302.

Harris, L.D. 1984. The fragmented forest. University of Chicago Press, Chicago.

Harvey, B., Leduc, A., Gauther, S. and Bergeron, Y. (2002) Stand-landscape integration in natural disturbance-based management of the southern boreal forest. *Forest Ecology and Management*. 155: 369-385.

Heliölä, J., Koivula, M., and Niemelä, J. (2001) Distribution of Carabid Beetles (Coleoptera,Carabidae) across a Boreal Forest-Clearcut Ecotone. *Conservation Biology* 15(2): 370-377.

Hély, C., Bergeron, Y., and Flannigan, M. D. (2000) Coarse woody debris in the southeastern Canadian boreal forest: composition and load variations in relation to stand replacement. *Canadian Journal of Forest Research.* 30(5): 674-687.

Hengeveld, R. (1979) Polyphagy, Oligophagy and Food Specialization in Ground Beetles (Coleoptera, Carabidae). *Netherlands Journal of Zoology*. 30 (4): 564-584.

Holliday, N.J. (1984) Carabid beetles (Coleoptera: Carabidae) from a burned spruce forest (*Picea* spp.). *Canadian Entomologist.* 116: 919.922.

Holliday, N.J. (1991) Species responses of carabid beetles (Coleoptera: Carabidae) during post-fire regeneration of boreal forest. *Canadian Entomologist.* 123: 1369:1389.

Holliday, N.J. (1992) The carabid fauna (Coleoptera: Carabidae) during postfire regeneration of boreal forest: properties and dynamics of species assemblages. *Canadia Journal of Zoology.* 70:440-452.

Huber, C., and Baumgarten, M. (2005) Early effects of forest regeneration with selective and small scale clear-cutting on ground beetles (Coleoptera, Carabidae) in a Norway spruce stand in Southern Bavaria (Höglwald). *Biodiversity and Conservation.* 14:1989-2007.

Huk, T. and Kühne, B. (1999) Substrate selection by Carabus clatratus (Coleoptera, Carabidae) and its consequences for offspring development. *Oecologia.* 121:348-354.

Hunter, M.L., Jacobson, G.L., Jr., and Webb, T III (1988) Paleoecology and the coarse-filter approach to maintaining biological diversity. *Conservation Biology*, 2(4): 375-385.

Hunter, M. L. 1993. Natural fire regimes as spatial models for managing boreal forests. *Biological Conservation.* 65: 115-120.

Huston, M. (1979) A General Hypothesis of Species Diversity. *The American Naturalist.* 113(1): 81-101.

Jacobs, J.M. (2006) Individual-based rarefaction using R package. University of Alberta Spence Lab R tutorials:
http://www.ales2.ualberta.ca/RR/spence_lab/index.asp?page=rarefaction

Jacobs, J.M., Work, T.T., and Spence, J.R. (2008) Influences of succession and harvest intensity on ground beetle (Coleoptera: Carabidae) populations in the boreal mixedwood forests of Alberta, Canada: species matter. In Back to the Roots or Back to the Future? Towards a New Synthesis between Taxonomic, Ecological and Biogeographical Approaches in Carabidology. *Proceedings of the XIII European Carabidologists Meeting*, Blagoevgrad, Bulgaria, August 20–24 2007. Edited by L. Penev, T. Erwin, and T. Assmann. Pensoft Publishers, Sofia, Bulgaria.

Klimaszewski, J., Langor, D.W., Work, T.T., Pelletier, G., Hammond, J.H.E., and Germain, C. (2005) The effects of patch harvesting and site preparation on ground beetles (Coleoptera, Carabidae) in yellow birch dominated forests of southeastern Quebec. *Canadian Journal of Forest Research.* 35(11) 2616: 2628.

Kneeshaw, D.D., Bergeron, Y., (1998) Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology*. 79 (3): 783-794.

Koivula, M. (2001) Carabid beetles (Coleoptera, Carabidae) in boreal managed forests – meso-scale ecological patterns in relation to modern forestry. Doctoral Thesis Summary, University of Helsinki. pp. 1-22.

Koivula, M. (2002) Alternative harvesting methods and boreal carabid beetles (Coleoptera, Carabidae). *Forest Ecology and Management.* 167: 103-121.

Koivula, M. and Niemelä, J. (2002) Boreal carabid beetles (Coleoptera, Carabidae) in managed spruce forests: a summary of Finnish case studies. *Silva Fennica.* 36, 423–436.

Koivula, M. and Niemelä, J. (2003) Gap felling as a forest harvesting method in boreal forests: responses of carabid beetles (Coleoptera, Carabidae). *Ecography*. 26: 179–187.

Koivula, M., Kukkonen, J., and Niemelä, J. (2002) Boreal carabid-beetle (Coleoptera, Carabidae) assemblages along the clear-cut originated succession gradient. *Biodiversity and Conservation.* 11**:** 1269–1288.

Koivula, M. and Spence, J.R. (2006) Effects of post-fire salvage logging on boreal mixed-wood ground beetle assemblages (Coleoptera, Carabidae). *Forest Ecology and Management.* 236: 102-112.

Kouki, J. Löfman, S. Martikainen, P., Rouvinen, S. and Uotila, A. (2001) Forest Fragmentation in Fennoscandia: Linking Habitat Requirements of Wood-associated Threatened Species to Landscape and Habitat Changes. *Scandinavian Journal of Forest research*. 16(3): 27-37.

Larochelle, A., and Larivière. M. C. (2003) A natural history of the ground-beetles (Coleoptera:Carabidae) of America north of Mexico. Pensoft Publishers, Sophia, Bulgaria.

Larrivée, M., Fahrig, L., and Darapeau, P. (2005) Effects of a recent wildfire and clearcuts on ground-dwelling boreal forest spider assemblages. *Canadian Journal of Forest Research.* 35: 2575–2588.

Latty, E.F., Werner, S.M., Mladenoff, D.J., Raffa, K.F., and Sickley, T.A. (2006) Response of ground beetle (Carabidae) assemblages to logging history in northern hardwood-hemlock forests. *Forest Ecology and Management.* 222: 335–347.

Legendre P. and Legendre L. (1998) Numerical Ecology, 2nd English edn. Elsevier, Amsterdam

Legendre P. and Gallagher, E. D. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia.* 129:271-280.

Lemieux, J.P. and Lindren, B.S. (2004) Ground beetle responses to patch retention harvesting in high elevation forests of British Columbia. *Ecography.* 27: 557-566.

Lindenmayer, D.B., Margules, C. R., and Botkin, D.B. (2000) Indicators of Biodiversity for Ecologically Sustainable Forest Management. *Conservation Biology.* 14(4) 941-950.

Lindroth, C.H. (1961-1969) The ground beetles (Carabidae excl. Cicindelinae) of Canada and Alaska. Parts I and II. *Opuscula Entomologica.* Pp.1-1192.

Lövei, G.L. and Sunderland, K. D. (1996) Ecology and Behavior of Ground Beetles (Coleoptera: Carabidae). *Annual Review of Entomology.* 41: 231-256.

Luff, M (2005) Biology and ecology of immature stages of ground beetles (Carabidae). *European Carabidology 2003. Proceedings of the 11th European Carabidologist Meeting.* DIAS Report, 114: 183-208.

Macdonald, S. E., Peters, V., Purdy, B.G., and Dale, M. (2001) SFMN Project: Natural regeneration of white spruce following natural disturbance in the western boreal forest. Sustainable Forest Management Network final report 2001-13: 1-17.

Macdonald, S. E., and Fenniak, T. E. (2007) Understory plant communities of boreal mixedwood forests in western Canada: Natural pattern and response to variable-retention harvesting. *Forest Ecology and Management.* 242: 34-48.

Martikainen, P., Siitonen, J., Punttila, P. Kaila, L. and Rauh, J. (2000) Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biological Conservation*. 94: 199-209.

Matveinen-Huju, K., Niemelä, J., Rita, H., and Hara, R.B. (2006) Retention-tree groups in clear-cuts: Do they constitute 'life-boats' for spiders and carabids? *Forest Ecology and Management*. 230: 119-135.

Matveinen-Huju, K. (2007) Doctoral dissertation: Short-term effects of variable retention on epigaeic spiders and carabid beetles in Finland. University of Helsinki. Finland. 2007. ISBN 978-952-92-1984-1 (paperback), ISBN 978-952-10-3894-5 (PDF)

McArdle, B.H. and Anderson, M.J. (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*. 82(1): 290-297.

McCune, B., and Grace, J.B. (2002) Analysis of ecological communities. MJM Software Design, Glenden Beach, Oregon.

McRae, D.J., Duchesne, L.C., Freedman, B., Lynham, T.J., and Woodley, S. (2001) Comparisons between wildfire and forest harvesting and their implications in forest management. *Environmental Review*. 9: 223–260.

Moore, J-D., Ouimet, R., Houle, D., and Camiré, C. (2004) Effects of two silvicultural practices on ground beetles (Coleoptera: Carabidae) in a northern hardwood forest, Quebec, Canada. *Canadian Journal of Forest Research*. 34: 959:968.

Niemelä, J. (1993) Interspecific competition in ground beetle assemblages (Carabidae): What have we learned? *Oikos*. 66(2):325-335.

Niemelä, J. (1997) Invertebrates and Boreal forest management. *Conservation Biology*. 11(3) : 601-610.

Niemelä, J., Haila,Y., Halme, E., Lahti, T., Pajunen, T. & Punttila, P. (1988) The distribution of carabid beetles in fragments of old coniferous taiga and adjacent managed forest. *Annales Zoologici Fennici*. 25: 107–119.

Niemelä, J., Spence, J.R., Langor, D.W., Haila, Y. & Tukia, H. (1993) Logging and boreal ground beetle assemblages on two continents: implications for conservation. In Gaston, K.J., New, T.R. & Samways, M.J. (eds.): Perspectives in insect conservation. Intercept Publishers Ltd., Andover, Hampshire. Pp. 29–50.

Niemelä, J. and Spence, J.R. (1999) Dynamics of Local Expansion by an Introduced Species: Pterostichus melanarius III. (Coleoptera, Carabidae) in Alberta, Canada. *Diversity and Distributions*. 5(4): 121-127.

Niemelä, J., Kotze, J., Ashworth, A., Brandmayr, P., Desender, K., New, T., Penev, L, Samways, M., and Spence, J. (2000) The search for common anthropogenic impacts on biodiversity: a global network. *Journal of Insect Conservation*. 4: 3-9.

Niemelä, J., Koivula, M. and Kotze, D. J. (2007) The effects of forestry on carabid beetles (Coleoptera: Carabidae) in boreal forests. *Journal of Insect Conservation*. 11:5–18.

Oksanen J., Kindt, R., and O'Hara B., (2005) The vegan package: Community ecology package version 1.6-10. R Project for statistical computing.

Oksanen, J. (2008) Multivariate analysis of ecological communities in R: vegan tutorial. Professional website: http://cc.oulu.fi/~jarioksa/opetus/metodi/vegantutor.pdf

Oliver, I. and Beattie, A.J. (1996) Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity. *Ecological Applications*. 6(2): 594-607.

Paquin, P. and Coderre, D. (1997) Changes in soil macroarthropod communities in relation to forest maturation through three successional stages in the Canadian boreal forest. *Oecologia*. 112:104-111.

Paquin, P. and Dupérré N. (2001) Beetles of the boreal forest: a faunistic survey carried out in western Québec. *Proceedings of the Entomological Society of Ontario* 132: 57-98.

Pearce, J.L., Venier, L.A., McKee, J., Pedlar, J., and McKenney, D. (2003) Influence of habitat and microhabitat on carabid (Coleoptera: Carabidae) assemblages in four stand types. *The Canadian Entomologist*. 135: 337 – 357.

Pearce, J.L. and Venier, L.A. (2006) The use of ground beetles (Coleoptera:Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: a review. *Ecological Indicators*. 6:780-793.

Peck, R.W., Niwa, C.G. (2005) Longer-term effects of selective thinning on microarthropod communities in a late-successional coniferous forest. *Environmental Entomology*. 34(3): 646-655.

Pedlar, J.H., Pearce, J.L., Venier, L.A. and McKenney, D.W. (2002) Coarse woody debris in relation to disturbance and forest type in boreal Canada. *Forest Ecology and Management.* 158: 189–194.

Pihlaja, M., Koivula, M., & Nemelä, J. (2006) Responses of boreal carabid beetle assemblages (Coleoptera, Carabidae) to clear-cutting and top-soil preparation. *Forest Ecology and Management*. 222: 182-190.

Poiani, K.A, Richter, B.D., Anderson, M.G, and Richter, H.E. (2000) Biodiversity Conservation at Multiple Scales: Functional Sites, Landscapes, and Networks. *BioScience.* 50(2): 133-146.

Proe, M.F., Griffiths, J.H., and McKay, H.M. (2001) Effect of whole-tree harvesting on microclimate during establishment of second rotation forestry. *Agricultural and Forest Meteorology*. 110:141–154.

R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rainio, J. and Niemelä, J. (2003) Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation*. 12 (3): 487-506.

Reeves, R.M., Dunn, G.A, and Jennings, D.T.(1983) Carabid beetles (Coleoptera: Carabidae) associated with the Spruce Budworm, Choristoneura fumiferana (Lepidoptera: Torticidae). *Canadian Entomologist.* 115: 453-472.

Roberts, D. W. (2006) The labdsv Package version 1.2-2. R Project for statistical computing.

Saint-Germain, M., Drapeau, P. and Hébert, C. (2004) Comparison of Coleoptera assemblages from a recently burned and unburned black spruce forests of northeastern North America. *Biological Conservation* 118: 583-592.

Saint-Germain, M., Larrivée, M., Drapeau, P., Fahrig, L, and Buddle, C.M. (2005) Short-term response of ground beetles (Coleoptera: Carabidae) to fire and logging in a spruce-dominated boreal landscape. *Forest Ecology and Management.* 212:118–126.

Schmiegelow, F.K.A., and Monkkonen, M. (2002) Habitat Loss and Fragmentation in Dynamic Landscapes: Avian Perspectives from the Boreal Forest. *Ecological Applications.* 12(2): 375-389

Siitonen, J., Penttilä, R. and Kotiranta, H. (2001) Coarse woody debris, polyporous fungi and saproxylic insects in an old-growth spruce forest in Vodlozero National Park, Russia Karelia. *Ecological Bulletins.* 49:231-242.

Simberloff, D. (1978). Use of rarefaction and related methods in ecology. In: Biological Data in Water Pollution Assessment: Quantitative and Statistical Analyses, eds Dickson K.L., Cairns J. Jr & Livingston R.J., pp. 150-165. American Society for Testing and Materials, Philadelphia, PA, U.S.A.

Simberloff, D. (1999) The role of science in the preservation of forest biodiversity. *Forest Ecology and Management.* 115: 101-111.

Simberloff, D. (2001) Management of Boreal Forest Biodiversity- A View from the Outside. *Scandinavian Journal of Forest Research Supplement.* 3: 105–118.

Similä, M., Kouki, J., Mönkkönen, M., & Sippola, A.L. (2002) Beetle species richness along the forest productivity gradient in northern Finland. *Ecography.* 25:42-52.

Spaulding, P. and Hansbrough, J.R. (1944) Decay of logging slash in the Northeast. Technical Bulletin 876, United States Department of Agriculture, Washington, District of Columbia, USA.

Spence, J.R. and Niemelä, J.K. (1994) Sampling carabid assemblages with pitfall traps: the madness and the method. *The Canadian Entomologist.* 126: 881-894.

Spence, J.R., Langor, D.W., Niemelä, J., Cárcamo, H.A. and Currie, C.R. (1996) Northern forestry and carabids: the case for concern about old-growth species. *Annales Zoologici Fennici.* 33: 173-184.

Spence, J.R. (2001) The new boreal forestry: adjusting timber management to accommodate biodiversity. *Trends in Ecology & Evolution.* 16(11): 591-593.

Spies, T. A., J. F. Franklin, and T. B. Thomas. (1988) Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology.* 69: 1689-1702.

Sturtevant, B.R., Bissonette, J.A., Long, J.N., and Roberts, D.W. (1997) Coarse Woody Debris as a Function of Age, Stand Structure, and Disturbance in Boreal Newfoundland. *Ecological Applications.* 7(2): 702-712

Tinker D.B. and Knight D.H. (2000) Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. *Ecosystems.* 3: 472-83.

Turner M.G., Baker W.L., Peterson C.J. and Peet R.K. (1998) Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems.* 1: 511-523.

Uliczka, H. and Angelstam, P. (1999) Occurrence of epiphytic macrolichens in relation to tree species and age in managed boreal forest. *Ecography.* 22:396-405.

Ulyshen, M.D., Hanula, J. L., Horn, S., Kilgo, J.C., and Moorman, C.E. (2006) The response of ground beetles (Coleoptera: Carabidae) to selection cutting in a South Carolina bottomland hardwood forest. *Biodiversity and Conservation.* 15:261–274.

Vance, C.C., and Nol, E. (2003) Temporal effects of selection logging on ground beetle communities in northern hardwood forests of eastern Canada. *Ecoscience.* 10: 49–56.

Van Dijk, T. S. (1996) The influence of environmental factors and food on life cycle, ageing and survival of some carabid beetles. *Acta Jutlandica* 71: 11-24.

Van Wagner, C.E., (1982) Practical aspects of the line intersect method. Petawawa National Forestry Institute, Canadian Forest Service Information Report PI-X-12.

Webb, A., Buddle, C., Drapeau, P., and Saint-Germain, M. (2008) Use of remnant boreal forest habitats by saproxylic beetle assemblages in even-aged managed landscapes. *Biological Conservation.* 141: 815-826.

Werner, S. M., and Raffa, K.F. (2003) Seasonal Activity of Adult, Ground-Occurring Beetles (Coleoptera) in Forests of Northeastern Wisconsin and the Upper Peninsula of Michigan. *American Midland Naturalist.* 149(1): 121-133.

Wikars, L. O. (1997) PhD thesis: Effects of forest fire and the ecology of fire-adapted insects. Faculty of Science and Technology, Uppsala University, Sweden.

Work, T.T., Buddle, C.M., Korinus, L.M., and Spence, J.R.(2002) Pitfall trap size and capture of three taxa of litter-dwelling arthropods: Implications for biodiversity studies. *Environmental Entomology*. 31(3): 438-448.

Work, T.T., Shorthouse, D.P., Spence, J,R., Volney, W.A.J., and Langor, D.W. (2004) Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the EMEND land base in northwestern Alberta. *Canadian Journal of Forest Research*. 34: 417-430.

Work, T.T., Koivula, M., Klimaszewski, J., Langor, D., Spence, J.R., Sweeney, J., and Herbert, C. (2008) An initial evaluation of carabid beetles as indicators of forest change in Canada using 10 large-scale forest experiments. *Canadian Entomologist*. 140: 393-414.

Yu, X.D., Luo, T.H., and Zhou, H.Z. (2006) Distribution of carabid beetles among regenerating and natural forest types in Southwestern China. *Forest Ecology and Management*. 231:169–177.